

# Headstands: a sexually selected signal in the swordtail fish *Xiphophorus nezahualcoyotl*

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(Accepted: 24 April 2008)

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## Summary

Behaviors associated with aggression in male–male competition may also be used in courtship. Headstands are performed by male *Xiphophorus nezahualcoyotl* during male–male interactions and by both males and females during courtship. This behavior consists of a descending vertical tilt of the head until the body is at a 45° to 90° angle with the substrate. We examined the function of headstands in male–male contests by investigating differences in their use by winners and losers, and correlations between headstands and other behaviors. We also investigated their function in mate choice by determining if females preferred videos of males performing headstands over videos of the same males not performing headstands. There was no correlation between performing the first headstand and biting first, or the total number of headstands and bites used. However, winners performed more headstands than losers in the second half of contests. We suggest that the headstand is an aggressive display providing information about Resource Holding Potential (RHP) in male contests. In addition, females had a significant preference for males performing headstands as compared to males that did not. We discuss the dual role of this behavior in sexual selection in relation to the information it may contain.

*Keywords:* male aggression, female preference, *Xiphophorus nezahualcoyotl*, headstands.

## Introduction

Darwin (1871) suggested that female mate choice and male–male competition are two processes through which traits evolve, and that these two mechanisms of sexual selection are mutually supportive (reinforcing), such that

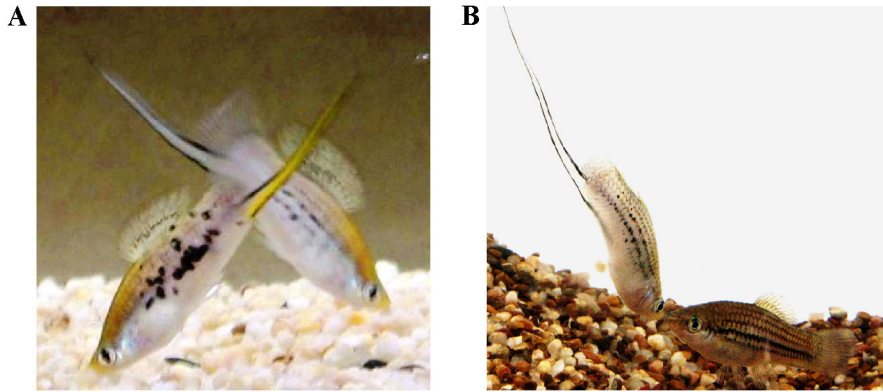
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the most attractive males are also the best competitors. While traits that have evolved through female mate choice could indicate direct benefits for the female, preferences can also evolve due to a genetic correlation between the behavior and the preference (e.g., Fisherian runaway model), or in a context other than mate choice prior to the male trait (Pre-existing Bias Hypothesis: Basolo, 1990; Endler & Basolo, 1998). Traits that have evolved through male–male competition could signal information about the fighting ability of the male (Kodric-Brown & Brown, 1984). In addition, sexual conflict theory (Parker, 1979) proposes that mate quality may not be positively correlated with intrasexual competitiveness, and there are an increasing number of cases demonstrating that the two mechanisms may select in different directions on the same traits (e.g., social pheromone in *Nauphoeta cinerea*: Moore & Moore, 1999; behavioral displays in *Chlamydera* bowerbirds: Borgia & Coleman, 2000; head elongation in *Prochyliza xanthostoma*: Bonduriansky & Rowe, 2003). Investigating the potential selection on a behavior used in courtship and male–male interactions can provide valuable insight into reinforcing as compared to conflicting selection on sexually selected male traits.

The headstand is a behavior used by *X. nezahualcoyotl* males during male–male interactions, by males during male–female interactions (Morris et al., in press), and by females, possibly as a receptive signal (Fernandez & Fernandez, in press), during male–female interactions. To perform a headstand, an individual hovers in the water and tilts vertically with its anterior end down and posterior end up at a 45° to 90° angle with the substrate (Figure 1). The initial description of the headstand was based on both field and laboratory observations (Morris et al., in press). Larger males performed more headstands, and the behavior was ranked as one that coaxes (i.e., courtship display) as opposed to coercing (i.e., sneak-chase) females to mate based on its negative correlation with attempted forced copulations (Morris et al., in press). Also in field observations, males that expressed the pigment pattern vertical bars, a sexually selected trait known to attract females in *X. nezahualcoyotl* (Morris et al., 2007), used significantly more headstands than males that did not express their bars when interacting with females (Morris et al., in press). These results suggest that headstands may function in both contexts of sexual selection in *X. nezahualcoyotl*; however this hypothesis has not been explicitly tested.

We examined the function of headstands in both male–male competition and in female mate preference for *X. nezahualcoyotl*. To examine the function of the headstand during male–male competition, we observed dyadic



**Figure 1.** (A) Male *X. nezahualcoyotl* performing headstands during a contest; (B) male *X. nezahualcoyotl* performing headstand to female *X. nezahualcoyotl* during courtship. This figure is published in colour at <http://www.ingenta.com>

male contests, compared the use of headstands to other behaviors, and compared the use of headstands among winners and losers as contests progressed. Previous studies of dyadic contests in several different species of *Xiphophorus* have found that contests consist of a display state, often followed by a more aggressive stage in which males bite, and that larger males are more often the winners of these contests (Morris et al., 1995; Moretz, 2003). We tested female preference for headstands using three pairs of videos of three males; one in which the male is performing sexual displays with headstands and one in which the same male is performing sexual displays without headstands.

## Materials and methods

### *Study organism*

Adult *Xiphophorus nezahualcoyotl* males and females were collected from the Río Salto (San Luis Potosí, Mexico) in December of 2005. They were transported back to Ohio University and three months later were isolated in individual 19-l aquariums for 9 months, during which time they were used in other behavioral studies. Two months before testing in the current study, males and females were transferred to 37-l communal aquariums containing a 1.3–1 female/male ratio of 7–9 individuals each. Individuals remained in

the communal aquariums for a minimum of one month before being physically and visually re-isolated in to 19-l aquariums for at least 14 days before the current study. All fish were kept on a 12 h light/12 h dark cycle and a daily diet of TetraMin<sup>®</sup> Tropical Flakes.

### *Male–male competition*

#### Contests

Ten pairs of *X. nezahualcoyotl* males were matched for pigment patterns and standard length, the length from the anterior most tip of the head to the posterior tip of the caudal peduncle (within a 6% difference in SL), and contests between the pairs of males were observed in February 2007. Paired males did not share an aquarium prior to the contests.

At least 20 h before the competition began, one male was placed on either side of a 37-l aquarium divided in half by an opaque barrier. The barrier was removable and, therefore, allowed some water to pass between the two compartments, potentially allowing transfer of olfactory cues. The males acclimated overnight and the following day they were allowed to acclimate to the placement of a video camera outside the tank for 10 min before removal of the dividing barrier. The contests were filmed until it was clear that the outcome of the contest had been decided (loser retreated with his dorsal fin relaxed and suppression of vertical bars). The contests were scored for duration, who performed the first “headstand” and “bite”, the number of bites and headstands each male used over the entire contest, and which male won the contest. Since all contests were not of equal length, contests were divided into halves to compare the use of headstands and bites across the progression of the contests.

#### Statistics

All analyses were performed using SPSS (ver. 14.0). Wilcoxon signed-ranks tests were used to compare differences in body size and behaviors between winners and losers, as well as to compare differences between the use of headstands and bites within contests. Spearman rank tests were used to determine if there were correlations between the number of headstands and number of bites for winners and losers, as well as the absolute size of the contestants and number of headstands, bites, and length of the contests.

*Female preference*

## Video production

Three focal males that varied in size (SL 32.89 mm, 38.5 mm, 40.92 mm) and pigment patterns were selected for videos to test for female preference for the headstand. These three males were excluded from the communal tanks but were used in male–male contests (see above). Filming occurred at least one week after the male–male contests. Filming occurred in a 190-l aquarium with the back, floor, and wall of the filming area lined in opaque plastic to create a uniform background. The entire aquarium measured 94 cm long and 30.5 cm wide. The filming area was reduced to a corner of the aquarium measuring 18 cm long and 17.8 cm wide. The reduced length and width of the filming area allowed us to place a stimulus fish in a Plexiglas holding box diagonal to the filming area. A video camera was set up 38 cm from and in front of the filming area. With this set up, the focal fish being filmed could see and interact with the stimulus fish; however, the stimulus fish was not included in the camera range. The focal male was placed in the aquarium the night before filming. An opaque divider was placed in front of the clear glass partition to block the filming area from the rest of the aquarium. Ten minutes before filming, a stimulus female was placed in the holding box. After the 10-min acclimation, the opaque partition was removed and the focal male was filmed for 10 min, at which point the opaque divider was returned, a stimulus male replaced the stimulus female in the holding box, and the procedure was repeated.

Males only performed headstands for females when a stimulus female was directly in front of the male, so it was not possible to film isolated focal males performing headstands to a female stimulus. Focal males performed headstands for stimulus males when the stimulus male was placed further from the focal male, allowing only the focal male to be filmed. The headstands males performed to one another appeared identical to the headstands used during courtship but are potentially different across the two contexts. Therefore, while the headstands were filmed in the context of male–male interactions by necessity, examining female preference for these headstands allowed us to determine if the display used in male–male competition is similar enough to evoke a response by females.

Film footage was edited using iMovie (Mac OS X). For each of the three males we made a pair of videos, a headstand video and a non-headstand

video, totaling six videos overall. In the non-headstand video, the individual male swam in front of the camera expressing vertical bars and an erect dorsal fin. The time of each swimming segment varied and was looped for each male. The headstand video of each pair of videos contained the same swimming segment but with a headstand segment spliced in between each loop. All videos began with 3 min of background color and lighting, but no fish, followed by a total of 9 min 40 s of stimuli. We determined that the size of the males females observed in the videos was within the range of normal *X. nezahualcoyotl* size by measuring the SL of the males in the videos on the choice test monitors (see below) at random intervals throughout the video. Video animations have been successfully used to test for female preferences in multiple species of fish (Reviewed by Rowland, 1999) including *Xiphophorus* (e.g., *X. helleri*: Rosenthal et al., 1996; Trainor & Basolo, 2000; *X. cortezi*: Morris et al., 2003; *X. continens*: Morris et al., 2005; *X. malinche*: Morris et al., 2006). By using three different males to make our three pairs of stimulus videos, we avoided over-generalizing our results to a potential aspect of the behavior, size or other morphological characteristic that interacted with the use of headstands by a particular male.

#### Choice tests

Twelve females, ranging in size from 38.2 to 42.6 mm SL, were tested for preference for headstands using the video animations described above. Choice tests were conducted in a 19-l aquarium that was visually divided into three 13 cm (approximately 3 body lengths) sections by two marked lines. The middle section was the neutral zone and the two end sections were association zones. The aquarium had a set-up similar to that found in Morris et al. (2003). We used high-resolution monitors positioned at opposite ends of the aquarium with the display screen framed by cardboard. Each monitor was attached to its own digital videodisc player. A mirror above the tank was diagonally tilted down to allow an observer to record the female's position in the tank.

At the start of each choice test, a female was placed in a clear Plexiglass container in the center of the middle (neutral) section of the tank. Opaque dividers blocked both video monitors. After a 10-min acclimation, the dividers were removed and the videos began, a headstand video played on one end of the tank and the non-headstand video of the same male played on the other end. After four minutes of viewing the videos (3 min lead-in which

the females were exposed to the background color and lighting and 1 min of male stimulus) the female was released from the holding container and allowed to swim freely for the rest of the video playing time. The amount of time the female spent in each visually marked section next to the monitors was recorded as association time for either video. At the end of the video playing time, the dividers were returned to block the monitors, the female was placed back in the clear Plexiglass container in the neutral zone, the videos were switched to the opposite ends of the tank, and the protocol was repeated in order to control for any female side bias. Seven to 9 days later, the test was repeated with the same female and a randomly selected different pair of videos. A different video pair, exhibiting a different male, was used in the second test to ensure that the female was responding to the headstand behavior, and not some other difference found in only one of the video pairs.

#### Statistics

We used one-way ANOVAs to determine if there were significant differences in the strength of preference (difference in the time spent with headstand and no headstand) across the three stimulus videos in the first and second tests. A paired Student's *t*-test was used to compare differences in the mean total time females associated with the Headstand and Non-Headstand videos summed across both tests. Combining the time the female spent with the headstand and no headstand treatments across two pairs of videos (made of two different males) provides a better estimate of female preference for headstands in general. The time a female spends associating with a male has been linked to male mating success in similar studies of the closely related species *X. nigrensis* (Ryan et al., 1990; Morris et al., 1992). A Spearman rank test was used to determine if there was a relationship between female size and strength of preference for headstands.

## Results

### *Male contests*

Only one of the ten contests did not involve headstands by either contestant. In two other contests, either the winner or loser did not perform headstands. Winners were as likely as losers to perform the first headstand (winner 3,

loser 4, same time 3). There was no relationship between being the first to use a headstand and the first to bite (Spearman's:  $\rho = -0.37$ ,  $df = 9$ ,  $p = 0.29$ ). In addition, there was no correlation between the number of headstands performed by the winners and losers of contests (Spearman's:  $\rho = 0.27$ ,  $df = 9$ ,  $p = 0.45$ ).

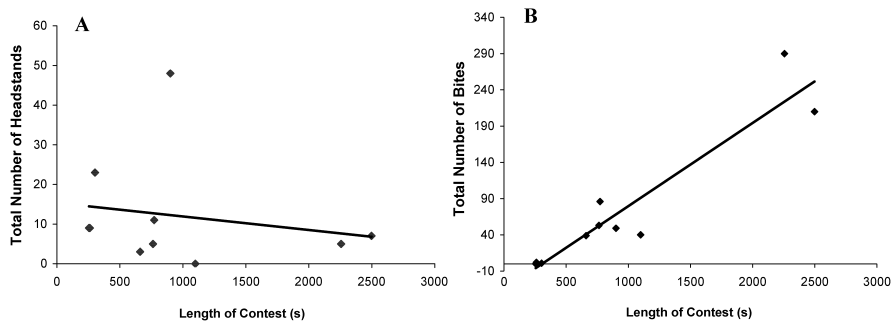
When contests were divided in half based on time, eventual winners and losers performed the same number of headstands in the first half. In the second half of contests, there was a significant difference in the number of headstands performed by winners and losers. This difference was a result of losers decreasing the number of headstands they performed in the second half, while winners continued to perform the same number of headstands across the two halves of the contest (Table 1).

One contest did not involve biting by either contestant, and in three other contests only the loser did not bite. There was a significant positive correlation in the number of bites between the winner and loser of a contest (Spearman's:  $\rho = 0.89$ ,  $df = 9$ ,  $p = 0.001$ ). This suggests that males in contests tended to match each other for number of bites. When contests were divided in half, losers performed significantly fewer bites than winners in the second half, but matched winners in the first half (Table 1).

There was no significant difference in the size between winners and losers (Table 1), with the larger male winning in five of the ten contests. Also, there was no significant relationship between percent size difference in males and contest length (Spearman's:  $\rho = -0.31$ ,  $p = 0.39$ ). These results were not surprising, as we had matched the males in the pairs to within 6% of

**Table 1.** Differences in size and behaviors by winners and losers across and throughout contests. Values are mean  $\pm$  SEM,  $Z$  and  $p$  scores were calculated using a Wilcoxon signed-ranks test. The number of bites and headstands by winners and losers were recorded for the first and second half of each contest.

		Winners	Losers	$Z$	$p$
Size (mm)		34.5 $\pm$ 1.4	34.1 $\pm$ 1.3	-0.36	0.72
1st half	Bites	10.6 $\pm$ 5.2	11.3 $\pm$ 6.2	-0.25	0.79
	Headstands	4.6 $\pm$ 1.9	3 $\pm$ 0.9	-0.65	0.51
2nd half	Bites	29.9 $\pm$ 9.9	24.7 $\pm$ 10.1	-2.2	0.02
	Headstands	3.6 $\pm$ 1.7	0.8 $\pm$ 0.5	-2.03	0.04



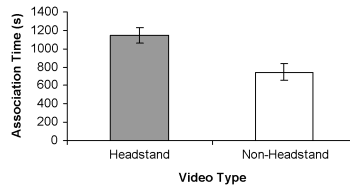
**Figure 2.** Total number of headstands (A) and bites (B) in relation to contest length.

one another in standard length. There was, however, a significant positive correlation between number of bites used by losers and the average size of the two males (Spearman's:  $\rho = 0.68$ ,  $p = 0.03$ ). This relationship was similar but not significant for the number of bites used by winners and average male size (Spearman's:  $\rho = 0.47$ ,  $p = 0.16$ ). No correlation was found between average size and number of headstands for winners or losers (Spearman's: winners  $\rho = -0.49$ ,  $p = 0.15$ ; losers  $\rho = -0.03$ ,  $p = 0.95$ ) or contest duration (Spearman's: winners  $\rho = 0.46$ ,  $p = 0.19$ ; losers  $\rho = 0.41$ ,  $p = 0.24$ ). These results suggest that while larger males used more bites when paired in contests, they did not use more headstands or take longer than pairs of smaller males to settle contests.

There was no detectable relationship between the number of headstands used in a contest (combined for winners and losers) and the length of the contest (Spearman's:  $\rho = -0.28$ ,  $p = 0.43$ ; Figure 2A). The number of bites used in a contest, on the other hand, was significantly greater in longer contests (Spearman's:  $\rho = 0.87$ ,  $p = 0.001$ ; Figure 2B).

#### *Female choice tests*

There was no significant difference in the strength of preference across stimulus videos in either the first or second tests (Test 1,  $F_{2,9} = 0.04$ ,  $p = 0.96$ ; Test 2,  $F_{2,9} = 1.1$ ,  $p = 0.37$ ), suggesting that all three pairs of videos elicited similar responses by the females. We detected a significant preference for the headstand videos as compared to the non-headstand videos (headstand:  $1144.7 \pm 87.51$ , non-headstand:  $745.8 \pm 90.01$  mean  $\pm$  SEM (s)); Paired sample  $t$ -test:  $t = 2.28$ ,  $df = 11$ ,  $p = 0.04$ , Figure 3). There was no



**Figure 3.** Female association time (mean  $\pm$  SEM (s)) with headstand (grey) and non-headstand (white) video treatments summed across preference tests with two different pairs of videos.

relationship between female size and strength of preference (Spearman's:  $\rho = -0.26$ ,  $p = 0.42$ ).

## Discussion

Headstands function to both attract females and as aggressive signals during male–male interactions in the swordtail *Xiphophorus nezahualcoyotl*, suggesting that this behavior is under reinforcing (Darwin, 1871), as opposed to conflicting (Parker, 1979), sexual selection. Females spent more time with the videos of males that were performing headstands, and during male–male interactions there was a significant difference between winners and losers in the use of headstands. While winners and losers performed the same number of headstands in the first half of the contests, in the second half of contests, only the losers significantly decreased the number of headstands they performed. These results are similar to those from a study of aggressive behaviors in cichlids (Jakobsson et al., 1979), where the differences between winners and losers in the frequency and types of aggressive behaviors did not differ until the last part of the contests. A comparable behavior, defined as a ‘head-down posture’, has been described for stickleback species. This behavior was considered an aggressive display as males often performed head-downs during territorial disputes until one male retreated to the middle of his territory (Wootton, 1976).

Behaviors used to both attract females and deter rival males could provide similar information about competitors and potential mates. Determining the type of information provided by a dual functioning behavior during male–male contests could help explain its evolution in attracting females. Because a headstand cannot physically harm the opponent, it is less aggressive than

a bite, and as a display behavior could provide information about the performer's motivation to fight (reviewed by Hurd & Enquist, 2001). *Xiphophorus* contests consist of a less aggressive (e.g., display) stage, followed by a more aggressive (e.g., bite) stage (Franck & Ribowski, 1987; Morris et al., 1995). The vertical bars display is considered a good indicator of aggressive motivation in many *Xiphophorus* species, as males always express their bars before contests escalate to biting, regardless of size or status (Moretz & Morris, 2003). In contrast, headstands were not always performed before a contest escalated to bites, and both winners and losers continued to perform headstands during the more aggressive stages of some contests. However, across the contests we observed, headstands became less common in the second half as compared to the first half for losers. Therefore, if headstands do convey information about motivation, it would be motivation to continue fighting, not to escalate the fight.

Game Theory suggests that competitors should not give away information on their intentions during contests (Maynard Smith & Parker, 1976; Maynard Smith, 1979). In other words, while displays used in contests may signal fighting ability or Resource Holding Potential (RHP), it is not to the advantage of the contestant to provide information about long-term intentions. Therefore, we suggest that losers should have matched winners in headstands as long as they were willing to continue fighting, but that they decreased the number of aggressive behaviors they performed because they had a lower ability to fight, or RHP. The difference in headstand frequency between winners and losers in the second, but not first half of contests is consistent with this hypothesis.

Signals used to assess RHP should be difficult to fake (Maynard Smith, 1979). If that were not the case, then all contestants could signal high RHP and receivers would soon evolve to ignore these signals. One way to keep signals honest is if there is a cost to signaling (Zahavi, 1975; Grafen, 1990). Energetic costs of the headstand may play a role in the decreased use of headstands by losers in the second half of the contests. Castro et al. (2006) found that oxygen consumption of winners increased after fights in *Betta splendens*. Similarly, Huntingford et al. (1995) found that in swimming crabs, oxygen consumption increased during and after fights and that after long fights, losers had higher respiration rates than winners. Both studies support the hypothesis that aggressive behaviors performed during fights carry

metabolic costs, and that these costs differ between winners and losers (Castro et al., 2006). Studies measuring respiration rates in contests and specifically the headstand in *X. nezahualcoyotl* may also reveal high energetic costs. If the headstand is energetically costly, it will act as a good signal of RHP for opponents to assess, particularly towards the end of the contest.

We found that all but one contest escalated to biting (although losers did not bite in a total of three contests). The contests were designed for symmetry in RHP through size matching ( $\leq 6\%$  size difference), social isolation, and lack of resource ownership in the competition aquarium. Escalation of contests is expected between contestants closely matched in RHP (Parker, 1974). With increased differences in RHP we would expect more contests to end without escalation to the biting stage.

Even though the opponents were matched for size within a contest, the sizes of the males used varied from 26 to 42 mm. We found that the number of bites by losers and winners increased as the absolute size of both the winner and loser of the contest increased. This relationship with male size was only significant with the number of bites by the loser, which is likely due to the fact that the losers decide when a contest will end and, therefore, only losers will have used their maximum preferred number of bites. Therefore, these results suggest that there is a positive relationship between male size and aggression in *X. nezahualcoyotl*.

Morris et al. (in press) suggested that during courtship, the headstand is one of the behaviors that ranks the highest on the coax to coerce continuum. This ranking was determined using the probability that an attempted copulation follows the behavior as an indicator of its function to coerce as compared to coax a female to mate. The headstand puts the male in a position that makes it difficult to attempt copulation. During male contests, headstands put the male in a position in which it seems it would be more difficult for a male to escape or deliver a bite as well. This observation strengthens the suggestion that the headstand is a signal that provides information about the strength of an individual male's RHP, since only individuals with higher RHP could afford to put themselves in a vulnerable position during a contest.

Even though headstands used by males in the context of courtship and male–male competition appear to be very similar, it is possible that the message delivered through the headstand varies in the different contexts. Our results provide some evidence to suggest that the headstands used in male–male competition are similar to those used in courtship. Because it was easier

to videotape a male doing headstands in response to a male than in response to a female, the headstands in our videotapes were in response to males, and we detected a significant female preference for the headstands in these videos. However, while Morris et al. (in press) found that males under 31 mm did not perform headstands towards females during courtship, in the current study 3 males under 31 mm (26 mm, 27 mm, 30.5 mm) performed headstands during male–male interactions. Therefore, the relationship between size and use of the headstands may differ when used in male–male interactions as compared to courtship.

Females also perform headstands when being courted by males and, therefore, the function of the headstand in courtship may be more interactive than revealed through our experiment design, requiring further study with techniques that examine male–female interactions. Patricelli et al. (2002) found that male bowerbirds increase courtship display intensity in response to behavioral signals from females so as not to startle females with overly aggressive displays. In this case it is suggested that female response and tolerance for courting intensity would be correlated with male attractiveness (Patricelli et al., 2003). Because the headstand is an aggressive display in male contests, during courtship, female response may serve as a regulator moderating the intensity and/or frequency with which males use this behavior. In the closely related swordtail fish *X. cortezi*, females performed significantly more headstands in the presence of preferred larger males, and the size of the male influenced his response to females performing headstands (Fernandez & Fernandez, in press). Morris et al. (in press) found that larger *X. nezahualcoyotl* males perform more intersexual headstands than smaller males. Perhaps the greater number of headstands by larger males is a function of increased female tolerance for this behavior by preferred larger males.

There is evidence of inter- and intrasexual use of the same trait in many different organisms. It has been argued that behaviors used in both inter- and intrasexual selection are more likely to have been co-opted from their original function in male–male competition by females for assessing mates because signals used in aggressive interactions are more reliable indicators of male quality (reviewed by Berglund et al., 1996). Currently, only two studies have successfully analyzed the phylogenetic origins of dual use traits (Borgia & Coleman, 2000; Morris et al., 2007) and, therefore, it is not yet possible to determine if there is a type of signal that is more likely to evolve in the context of competition as compared to courtship. The skrraa call in bowerbirds

is an aggressive signal that evolved in the context of male–male competition and was co-opted by females for use in mate choice, possibly as a signal of male quality (Borgia & Coleman, 2000). On the other hand expression of vertical bars in swordtail fishes was co-opted from mate choice to male competition, where it functions as a signal of intention to attack (Morris et al., 2007). As headstands do not appear to function as a signal of aggressive motivation in male–male contests, but are used by both males and females during courtship, it will be instructive to determine the context in which this signal initially evolved. Future phylogenetic analysis and empirical testing on the use of the headstand throughout *Xiphophorus* will reveal its evolutionary pattern and ways in which it has been modified since its origin.

#### Acknowledgements

We would like to thank Scarlett Tudor, Natalie Dubois, Andre Fernandez, Donelle Robinson and Jason Brewer for input, guidance and cooperation. We also thank the Republic of Mexico for permission to collect fish (permit No. DAN 02031), and the National Science Foundation for grants to M.R.M. (IBN-9807925 and IBN-9983561). All experiments comply with current laws and with the Animal Care Guidelines of Ohio University (Animal Care and Use approval number L01-01).

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