

# Male Mating Tactics in the Northern Mountain Swordtail Fish (*Xiphophorus nezahualcoyotl*): Coaxing and Coercing Females to Mate

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## Abstract

Our understanding of the evolution of alternative male mating tactics would benefit greatly from more comparative studies; however, descriptions of the variation in mating behaviors are often lacking or reported in ways that consider only the role of male–male competition. Here we examine the mating behavior of the swordtail fish *Xiphophorus nezahualcoyotl* in relation to male size across different competitive contexts and in relation to coaxing vs. coercing females to mate. We also compare these results with reports for four other species of northern swordtails. The mating behaviors displayed by *X. nezahualcoyotl* males were correlated with male size, and were ranked in order from most coaxing to most coercive (a new behavior ‘headstand’, frontal displays, backing and fast chase) based on the probability that a behavior was followed by an attempted forced copulation. The largest males never used the most coercive behavior in the laboratory setting, even in the context of a larger competitor, and the smallest males never used the most coaxing behavior, even when alone with females. We argue, however, that changing the competitive context may not be the best way to expose the full range of behaviors a male may use if circumventing female mate choice is also driving the evolution of the alternative tactics. Finally, when we compared the mating behaviors of *X. nezahualcoyotl* males to those of the males of four other species of northern swordtails, they were not most similar to males of the closely related species *X. continens*. In *X. continens*, all males are small and have no morphological traits or behaviors that coax females to mate, where as even the smallest *X. nezahualcoyotl* males had both morphological and behavioral traits that could coax females to mate.

## Introduction

Alternative mating strategies are expected to evolve when there is strong sexual selection on males; males that are not good competitors or less likely to be preferred by females would be selected to use behaviors that allow them to circumvent both

male–male competition and/or female mating preference (Shuster & Wade 2003). Therefore, it is often assumed that the more sneaky, coercive mating behaviors evolved after the behaviors in which males monopolize and coax females to mate (although see Ptacek et al. 2004). When alternative strategies have been considered in a phylogenetic

context (Mank & Avise 2006a,b), the focus has been on the effect of male–male competition on tactics (bourgeois, parasitic and cooperative) rather than female mate choice. However, to determine how and when coercive behaviors evolved in relation to coaxing behaviors, or to evaluate the relative roles of male–male competition and female mate choice in driving the evolution of alternative mating tactics, alternative tactics should be considered not only in the context of circumventing male–male competition but in relation to circumventing female mate choice as well. By documenting alternative mating behaviors of several closely related species in both contexts of sexual selection it will be possible to determine the ancestral states as well as relative roles of female mate choice and male–male competition in the evolution of alternative tactics. In this study we examine the mating tactics of the swordtail *Xiphophorus nezahualcoyotl*, and compare them with the tactics of other swordtail species that have been studied to date.

Swordtails and platyfishes (*Xiphophorus*) have been studied extensively in relation to their systematics, biogeography, genetics, oncology and behavior (reviewed in Meffe & Snelson 1989) and are an excellent system in which to study the evolution of alternative mating behaviors from both the perspective of female mate preference and male–male competition. Sexual conflict clearly plays an important role in livebearing fishes because of the evolution of internal fertilization (Arnqvist & Rowe 2005); while male–male competition does occur, female mate choice is also prevalent. The alternative mating behaviors in *X. nigrensis* and *X. multilineatus* have been studied extensively, and represent one of the few examples of alternative strategies (sensu Gross 1996) characterized by a genetic polymorphism. Male mating behaviors in both *X. nigrensis* and *X. multilineatus* are tightly linked to alleles of a Y-linked gene (*P*) that controls the size at which males reach sexual maturity. As males grow very little after sexual maturity, the early-maturing males remain small and use a sneak–chase behavior: sneaking to avoid detection by larger competitors and chasing female to force copulations. Late-maturing large males engage in male–male competition to gain access to territories where females feed (Morris et al. 1992) and court females (Zimmerer & Kallman 1989; *X. multilineatus* is referred to as *X. nigrensis* in this study; Ryan & Causey 1989, *X. nigrensis*). Detailed descriptive studies of the variation in male mating behavior in relation to size across most of the other species in *Xiphophorus*, however, are lacking.

*Xiphophorus nezahualcoyotl* (Rauchenberger et al. 1990) is a member of the northern swordtail clade, as well as of the smaller *montezumae* clade which includes *X. montezumae* and *X. continens* (Rauchenberger et al. 1990; Morris et al. 2001). Within the *montezumae* clade, males of *X. montezumae* have a body size similar to that of *X. nezahualcoyotl* males, which is relatively large (when compared with other swordtail species), while *X. continens* males are all small and have no morphological traits or behaviors that coax females to mate (Morris et al. 2005). Kallman (1983) determined that there were two Y-linked *P*-alleles for *X. nezahualcoyotl* (referred to as *X. montezumae*); allele 's' for maturation at a small size (26–41 mm) and allele 'L' for maturation at large size (29–50 mm). The broad overlap in sizes was attributed to environmental conditions, as the two genotypes did not overlap in size when raised under identical conditions (30–36 and 39–49 mm; Kallman 1989). Two studies have examined male and female responses to the pigment pattern 'vertical bars' within the context of a larger comparative study (Moretz & Morris 2006; Morris et al. 2007). *X. nezahualcoyotl* females preferred males with vertical bars (Morris et al. 2007), but the timing of the expression of vertical bars in male–male contests suggested that it was not a honest signal of intent to attack, and males had either weak or no response to this sexually selected signal (Moretz & Morris 2006).

In this study, we compare the mating behaviors and sexually selected morphological traits of *X. nezahualcoyotl* with those of four other species of *Xiphophorus*, and describe a new behavior not previously reported for this group of fishes. We examine the relationship between male size and mating behaviors by quantifying the behavioral repertoire of males in a controlled laboratory setting, with and without competitors, as well as in the field. Each mating behavior is also assessed in relation to its role in coercing when compared with coaxing females to mate. Finally, we examined the presence of the sexually selected traits, the sword and vertical bars, in relation to male size and the use of coaxing and coercive mating behaviors.

## Methods

All field observations were conducted in Río Salto, San Luis Potosi, Mexico in 2003 and 2004. Fish brought back to the laboratory for further study were collected either after field observations were completed during a given field trip, or from a different location in the same river. All fish caught were

measured for standard length and sword length, and scored for sex (females, males, juveniles) before being returned to the river or brought back to the laboratory for behavioral studies.

### Description of Mating Behaviors

We examined the mating behaviors of 15 male–female pairs using the same protocol as that of Ryan & Causey (1989) and Morris et al. (2005), so that we could compare the mating behaviors of *X. nezahualcoyotl* with those of other species of swordtail fishes (see Table 1 for a description of the behaviors scored). Because of logistical considerations (the extended period of time that large males take to mature) the 10 ‘large’ males (>34 mm) were wild-caught, while the five ‘small’ males (<26 mm) were born and raised in the laboratory. Even though there can be extensive overlap of the two genotypes of males previously identified for this species, especially when raised in different environments (Kallman 1983, 1989), no males with the ‘L’ allele in previous studies were smaller than 29 mm, and so we assumed that all males classified as ‘small’ in our study had the ‘s’ allele. It is possible, however that some of the smallest males that we classified as

‘large’ may have actually had the ‘s’ allele, as a few of the males with the ‘s’ allele were larger than 34 mm in previous studies. One male was placed in the center of a 75.7 l test aquarium and a randomly selected female was placed in an opaque tube in the middle of the same aquarium. Both fish were allowed to acclimate for 10 min. The female was released from the tube by a pulley system from an adjacent room, and the interactions between the male and female were videotaped for 10 min. The videotapes were then examined to score the number of ‘attempted copulations’, ‘fast chases’, ‘frontal displays’, ‘headstands’, ‘backing’, ‘circles’, and ‘nibbling’ directed at the female, as well as whether or not the vertical bars were expressed.

### Contextual Use of Male Mating Behaviors

We conducted the following experiment to determine if the mating behaviors males expressed were related to male size, and how the behaviors a male exhibited changed depending on the presence of a larger male competitor. Behaviors that only function to circumvent male–male competition should be much less common when a male is alone with a female. However, one may or may not expect coercive behaviors to be expressed when alone with a female, depending on how females discriminate among males and how successful a male is once it enlists female cooperation. We observed 14 males alone with three females in a 227-l aquarium, and 13 of these 14 males with the same three females and a competitor that was more than 5 mm larger than the focal male. Seventeen females were used overall as stimuli (range 30.8–39.6 mm,  $x \pm SD = 32.4 \pm 4.87$  mm), with each female being used two to three times. The females were assigned to each male randomly. Half of the males were tested with the females and the larger competitor first, and half with the females and no competitor first. If male–male competition drives the evolution of alternative mating strategies in this species, we would expect males to use the most coaxing behaviors of their behavioral repertoire when alone with females, while in the competitive context, we expected males to use the most coercive behaviors of their behavioral repertoire.

The focal male was separated from the females and the larger male (when present) with an opaque divider for a 10-min acclimation period, and then the divider was removed for the 10-min observation period. During the observation period, the numbers of the following behaviors directed at a female were

**Table 1:** Description of mating behaviors of male *Xiphophorus* species

Attempted copulations	Male orients itself next to or behind female, brings its gonopodium to a forward position and attempts to insert it into the female's gonopore. These attempted copulations are considered forced as the female swims away from male
Fast chases	Male darts quickly towards a female and follows her for a period of one to several seconds, attempting to copulate
Frontal display	Male curves its body into a ‘C’ and quivers back and forth while positioned in front of female (included ‘figure eight’ display if male switched the side presented toward female)
Headstands	While in front of female the male tilts vertically with his head pointed downward, body forming a 45° or greater angle to the substrate
Backing	Male begins by facing away from the female, often within one body length anterior to it, and then swims backward in the direction of the female; often repeated several times
Circle	Male swims numerous tight circles around the female
Nibbling	Male nips at female's gonopore
Expression of vertical bars	Males darken vertical bar pigment pattern when interacting with females

recorded: backing, frontal displays, headstands, fast chases and attempted forced copulations (Table 1). No gonoporal nibbling or circling was observed. Attempted copulations were considered 'forced' when the female would respond by swimming away rapidly. Cooperative copulations are very rarely observed in the laboratory, and all the attempted copulations we observed were 'forced'. In observations that included a larger competitor, the number of bites the larger male directed toward the smaller one was also recorded.

### Field Observations of Mating Behaviors

Focal observations were conducted in Río Salto in March 2003 and 2004. Observations were made using a mask and snorkel with a plastic board and pencil for recording data underwater. A 1-m<sup>2</sup> area (quadrant) was estimated by using a 1-m-long rope as a guide. Right before initiating a focal observation, we counted the numbers of males (distinguishable by the presence of a gonopodium), females (distinguishable by the presence of a brood spot and the lack of a gonopodium), and juveniles/unknowns (having neither a gonopodium nor brood spot) within the area, after which the focal male was chosen. These counts provided a one-time snapshot of the number of other individuals on the quadrant. Males were not marked, and therefore we made the assumption that when we moved to a new area (which involved swimming several meters away) we were observing a different male. Based on the distances males moved while defending an area during focal observations (approx. 1 m<sup>2</sup>), this is likely to be a safe assumption. The standard length of the focal male was estimated as 'large' (>40 mm) or 'small' (<40 mm) relative to a 40 mm line drawn on the plastic board. Although it is not possible to know if these size classes match the two genotypes identified by Kallman (1983, 1989) for this species, based on the sizes of the two genotypes when raised in similar conditions (Kallman 1989) most of the males considered 'small' should have carried the 's' allele and most of the males considered large the 'L' allele. The number of headstand, backing, frontal displays and fast chases were noted (see description of behaviors in Table 1). Male–male interactions were also observed, and the relative size of the second male was noted as being larger, smaller, or similar to the size of the focal male. The frequencies of chases, retreats, and aggressive displays (primarily circling with dorsal fins erect) in male–male interactions were recorded. Even though all males in this

species examined so far have vertical bars, there were males in the field without their bars expressed. Therefore, we noted the context in which focal males had their bars expressed. Observations were conducted for 10 min or until the focal male swam out of the area.

We compared the number of females on a quadrant between the small and large males with a Mann–Whitney U-test to determine if larger males had access to more females than smaller males. For each of the behaviors observed, we calculated a rate by dividing the number of behaviors observed by time observed. We compared the rates of these mating behaviors across the two size classes of males with Mann–Whitney U-tests. We also compared the rate of chases and aggressive displays (dominant behavior) across male size classes with the rate of retreats (submissive behavior) to determine if larger males were more likely to use dominant behaviors when compared with smaller males. In addition, we examined the relationship between the number of males and the number of females on a male's quadrant to the male's rate of mating behaviors, with Spearman's rank correlation tests.

## Results

### Description of Mating Behaviors

The sizes of the 'large' (>34 mm) wild-caught males observed in this experiment ranged from 34.2 to 45.7 ( $x \pm SD = 40.3 \pm 3.47$  mm) and they were paired with females that ranged from 30.8 to 39.6 mm ( $x \pm SD = 35.2 \pm 3.08$  mm). The sizes of the 'small' laboratory-born males ranged from 21.7 to 25.2 mm ( $x \pm SD = 23.7 \pm 1.44$  mm), and they were paired with females that ranged from 38.2 to 39.5 mm ( $x \pm SD = 39.0 \pm 0.7$  mm). The size of the female was significantly correlated with the total number of behaviors the males used (Pearson's correlation =  $-0.687$ ,  $p = 0.005$ ,  $n = 15$ ). Therefore, as the females tested with the small males were significantly larger (t-test, equal variances not assumed,  $t = 3.7$ ,  $df = 10.7$ ,  $p = 0.004$ ), we did not compare the number of behaviors the males used in this experiment between size classes. In addition, as the sizes of females used in previous studies were not reported, we only compare the presence/absence of behaviors (not number of behaviors per minute) across species between size classes (see Table 2).

We observed a new behavior not previously described for *Xiphophorus* fishes that we have named 'headstands'. Eight of the 10 'large' males performed

**Table 2:** Comparison of male behaviors by size in non-competitive mating trials with one female

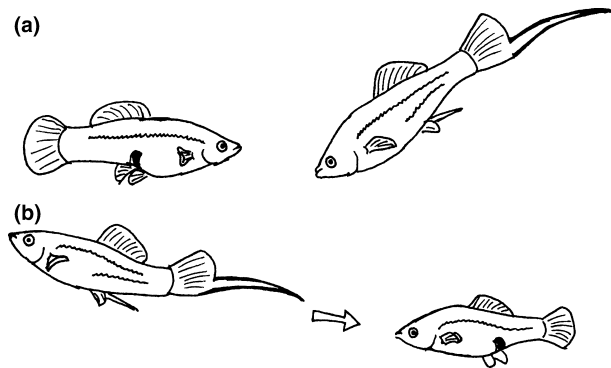
Behaviors	<i>nezahualcoyotl</i>		<i>continens</i>	<i>pygmaeus</i>	<i>nigrensis</i>		<i>multilineatus</i> <sup>b</sup>	
	Small	Large	Small	Small	Small	Large	Small	Large
Fast chases	+	+	+	+	+	+ <sup>a</sup>	+	0
Nibbling	0	0	+	0	0	0	0	0
Attempted copulations	+	+	+	+	+	+	+	0
Circle	0	0	0	+	0	0	+	0
Frontal display	+	+	0	0	+	+	+	+
Backing	+	+	0	0	NR	NR	0	+ <sup>a</sup>
Headstands	0	+	0	0	0	0	0	0
Expression of vertical bars while courting	+	+	NA	NA	NA	NA	NA	+

Large *X. nezahualcoyotl* males observed were over 34 mm (n = 10), while small males were under 26 mm (n = 5, current study), and are compared with *X. continens* (Morris et al. 2005), *X. pygmaeus* and *X. nigrensis* (only the smallest and largest size classes, Ryan & Causey 1989) and *X. multilineatus* (Zimmerer & Kallman 1989).

+ = reported as present; 0 = reported as absent; NR = not reported; NA = not applicable (males do not have vertical bars).

<sup>a</sup>Rare (only one male used one fast chase, and backing was noted as occurring occasionally, but not scored).

<sup>b</sup>Males were observed for 30 min while all other observation periods were 10 min.



**Fig. 1:** Drawings of male *Xiphophorus nezahualcoyotl* performing the courtship behaviors (a) 'headstand' and (b) 'backing'.

'headstand' during courtship, while none of the five 'small' males used headstands. In a headstand, the male slowly tilts vertically such that its head is pointed downward, with its body forming approximately a 45° or greater angle with the substrate. Often, the sword was slightly curved to one direction, typically away from the female (Fig. 1a). The male held this position for an average of about 5 s, and this behavior was typically initiated directly in front or to one side of the female's head. If the female was in motion, the male sometimes followed it in an upward or downward direction while holding this position.

Five of the 10 'large' and one of the five 'small' males performed backing behavior, which has been described for various species of *Xiphophorus* (Heinrich & Schroder 1986; Haas 1993; Basolo & Alcaraz-Zubeldia 2003). The male begins by facing away

from the female, often directly anterior to her, and then swims backward in her direction. Although contact was not made, the subjective appearance of this behavior was that the male attempted to poke the female in the head with its sword (Fig. 1b). This behavior was most often repeated several times in succession.

The mating behaviors of small *X. nezahualcoyotl* were not more similar to those of *X. continens* (Table 2) than to the small males of any of the other species. Gonoporal nibbling was only seen in *X. continens*, while frontal display was not observed in *X. continens* or the other species that has only small males, *X. pygmaeus*. Fast chases were used by the small males in all of the species. Large males of *X. multilineatus* and *X. nigrensis* have a body size that is relatively similar to an average-size *X. nezahualcoyotl* male, while small males of *X. multilineatus* and *X. nigrensis* have a body size relatively similar to a small-size *X. nezahualcoyotl* male. When the 'large' *X. nezahualcoyotl* males are compared with the large *X. nigrensis* and *X. multilineatus* males (Ryan & Causey 1989; Zimmerer & Kallman 1989; Table 2), what is most notable is the use of fast chase and headstand, which are missing from the behavioral repertoire of the large males of these other two species.

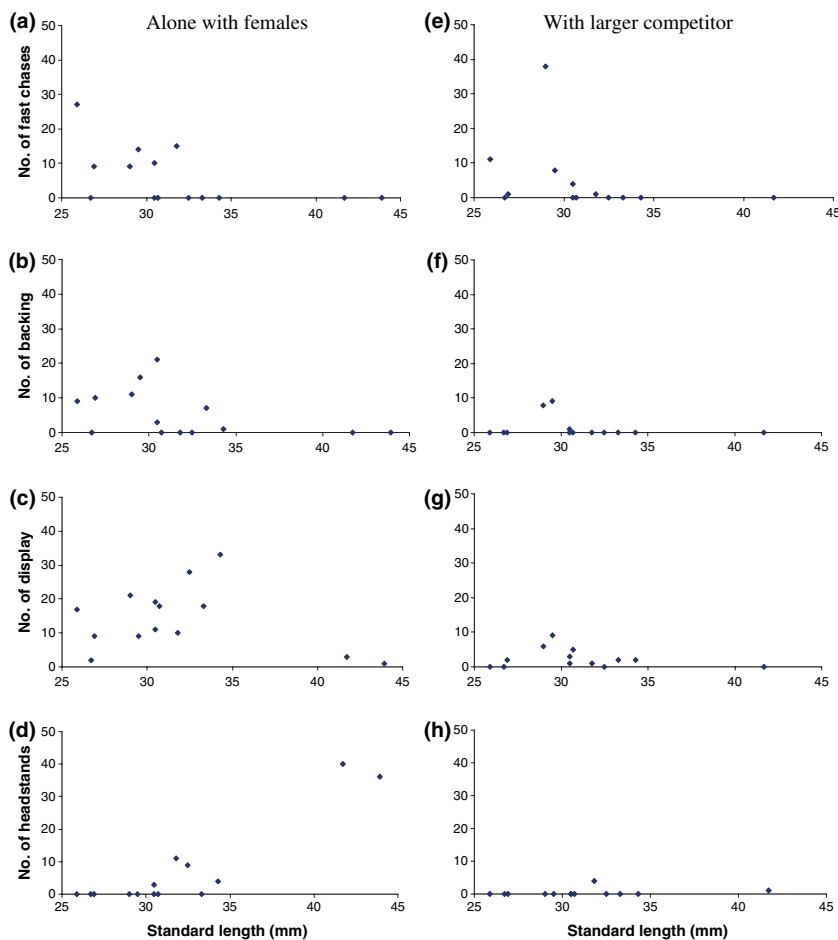
Because of limited visibility in the videotapes and through the one-way glass, bar expression in males was difficult to discern. All the males in this species have bars, and close observation of the videos confirmed bar expression in six males. Bar expression was likely but uncertain in two additional males and absent in two other males.

## Contextual Use of Male Mating Behaviors

The mean standard length of the 14 focal males was 31.9 mm (SD = 5.23 mm) and ranged from 25.9 to 43.9 mm. When focal males were alone with three females, the frequency of fast chases was negatively correlated with male size ( $r = -0.56$ ,  $n = 14$ ,  $p = 0.04$ , Fig. 2a), and there was a negative trend between backing and male size ( $r = -0.50$ ,  $n = 14$ ,  $p = 0.068$ , Fig. 2b), that was not statically significant. The number of frontal displays and headstands the focal males used were both positively correlated with male size (frontal displays:  $r = 0.58$ ,  $n = 14$ ,  $p = 0.03$ , Fig. 2c; headstand:  $r = 0.76$ ,  $n = 14$ ,  $p = 0.002$ , Fig. 2d). Using a significant positive correlation with attempted forced copulations as an indicator of a coercive mating behavior, both fast chase ( $r = 0.55$ ,  $n = 14$ ,  $p = 0.04$ ) and backing behavior ( $r = 0.851$ ,  $n = 14$ ,  $p = 0.0001$ ) would be classified as coercive behaviors. On the other end of the extreme, headstands ( $r = -0.66$ ,  $n = 14$ ,  $p = 0.01$ )

and frontal displays ( $r = -0.59$ ,  $n = 14$ ,  $p = 0.02$ ) were significantly negatively correlated with attempted forced copulations, and thus would be classified as coaxing behaviors.

One of the focal males observed alone with three females (43.9 mm standard length, SL), was not tested with the larger competitor. The mean standard length of the larger competitor males was 39.7 mm (SD = 5.08 mm) and ranged from 32.5 to 43.9 mm. Of the six males that used fast chase when no other male was present, five of these used fast chase in the presence of the competitor, in addition to one more male that did not chase when alone with the females (Fig. 2e). Four of the 13 males increased the number of fast chases used when with the competitor. Overall, there was no significant difference in the use of fast chase between being alone with the females and with a larger competitor (Table 3). The focal males decreased the use of backing (Fig. 2f), frontal displays (Fig. 2g) and headstand (Fig. 2h) in the presence of a larger competitor as



**Fig. 2:** The number of behaviors a male used when alone with three females (a–d) when compared with the number used when with three females and a competitor (e–h) as a function of standard length (mm).

**Table 3:** Comparing the frequency of behaviors (number/minute) of the focal males when alone with three females to being in a competitive situation with a larger male and three females

Behavior	Alone	With competitor	Z	p	B-H critical
Fast chase	6.49	4.84	-1.01	0.31	0.025
Backing	6.00	1.38	-2.52	0.01 <sup>a</sup>	0.0125
Frontal display	15.23	2.38	-3.06	0.002 <sup>a</sup>	0.006
Headstands	5.15	0.38	-2.02	0.04	0.01875

All probability values are two-tailed (Wilcoxon signed rank test); df = 12 for all tests.

p-values and critical values for multiple comparisons using Benjamini-Hochberg (B-H) procedure (Thissen et al. 2002).

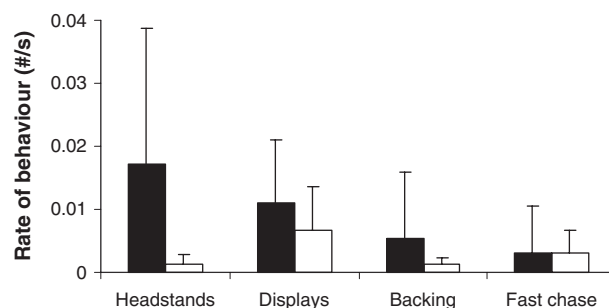
<sup>a</sup>Statistically significant based on the B-H critical value.

compared to when they were alone; when corrected for multiple tests, backing and frontal displays were significant, while headstands was not (Table 3). Even though the average rates of male coaxing behaviors changed when with a competitor as compared to alone, there were individual males that did not use the full spectrum of mating behaviors in either context. The largest males did not use fast chase when alone or with a competitor (>32 mm, Fig. 2), and the smallest males did not use headstand (<31 mm, Fig. 2). It is possible that these two behaviors are linked to the 's' and 'L' allele. However, 'L' allele males can be as small as 29 mm, and 's' allele males as large as 41 mm, and therefore it cannot be ruled out that males of both genotypes use both fast chases and headstands.

### Field Observations of Mating Behaviors

We made six focal observations in 2003 (all males larger than 40 mm) and 16 in 2004 (seven larger than 40 mm and nine smaller). The mean number of males per quadrant was 1.8, and the average number of females was 4.7 (SD = 3.86). Number of males on a quadrant was positively correlated with the number of females ( $r = 0.63$ ,  $n = 22$ ,  $p = 0.002$ ). The number of females on the quadrants of the large males (mean number of females  $\pm$  SD =  $5.6 \pm 4.00$ ) when compared with the number of females on quadrants of the small males (mean number of females  $3.3 \pm 3.42$ ) was not significant different ( $Z_{13,9} = -1.2$ ,  $p = 0.21$ ).

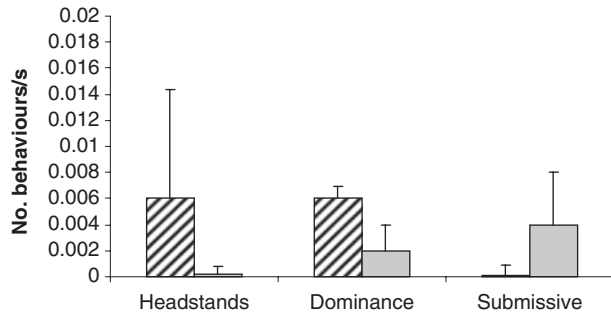
The average observation time per focal male was 7.9 min (SD = 2.68). When we compared rates of behaviors (number per minute) for the larger vs. smaller males, larger males had a higher rate of headstands than smaller males ( $Z_{13,9} = -2.25$ ,  $p = 0.03$ , Fig. 3); however, there were no other differences in the rates of the behaviors used by smaller



**Fig. 3:** Rates (frequency/minute) of headstands, displays, backing and fast chase behavior in field for large (■, >40 mm) when compared with small (□, <40 mm) males.

and larger males (frontal display rate:  $Z_{13,9} = -0.97$ ,  $p = 0.36$ ; backing rate:  $Z_{13,9} = -1.0$ ,  $p = 0.36$ ; fast chase rate:  $Z_{13,9} = -1.5$ ,  $p = 0.13$ , Fig. 3). As the number of behaviors a male used was influenced by the size of the female in the one male/one female laboratory study, we also considered the proportion of males that used fast chase (six of nine smaller males, or 67%; three of the 13 larger males, or 23%), and found that a greater proportion of smaller males used fast chase (contingency table:  $\chi^2_1 = 4.18$ ,  $n = 22$ ,  $p < 0.05$ ). We did not detect a relationship between size and the use of headstands (nine of 13 smaller males, 69%; four of nine larger males, 44%; contingency table:  $\chi^2_1 = 1.35$ ,  $n = 22$ ,  $p = 0.25$ ). Five individuals (three smaller and two larger) used both headstands and fast chase.

The context in which males expressed their vertical bars was recorded for 15 of the 16 focal observations made in 2004. Eight males had their bars expressed while interacting with females and six of those eight also expressed their bars while interacting with males. Males that expressed their bars while interacting with females had on average a higher rate of headstands than males that did not ( $Z_{8,7} = -2.9$ ,  $p = 0.004$ , Fig. 4). Males that expressed their bars while interacting with other males had on average a higher rate of dominant behaviors (chases + aggressive displays;  $Z_{8,6} = -2.03$ ,  $p = 0.04$ , Fig. 4) and a lower rate of submissive behaviors (retreats;  $Z_{8,6} = -2.02$ ,  $p = 0.04$ , Fig. 4) than males that did not. Finally, males that expressed their bars while interacting with other males were on quadrants with fewer females (mean number of females  $\pm$  SD =  $1.67 \pm 0.516$ ) than males which did not express their bars (mean number of females  $\pm$  SD =  $5.5 \pm 4.69$ ;  $Z_{8,6} = -2.1$ ,  $p = 0.03$ ). The same was not true for males that expressed their bars while interacting with females (bars on, mean number of females  $\pm$  SD =  $2.75 \pm 2.60$ ; bars off,



**Fig. 4:** Comparison of males that had their bars expressed (▨) and those that did not (■) for rate of headstands (when interacting with females), dominant behaviors (chasing and displaying to other males) and submissive behaviors (fleeing when being chased by another male).

mean number of females  $\pm$  SD =  $6.3 \pm 5.38$ ;  $Z_{8,7} = -1.54$ ,  $p = 0.12$ ).

Fifty-five males were captured and measured in the field and their mean standard length was 39.1 mm (SD = 11.18 mm), ranging from 22.8 to 64.4 mm. Males were identified by the presence of fully formed gonopodium. Seven males did not have a sword and their mean standard length was 27.9 mm (SD = 2.13 mm), ranging from 24.8 to 31.5 mm. Rauchenberger et al. (1990) only reported sword indices (length of sword/standard length) for males that had been sexually mature for 12 mo in the laboratory. Standardizing for the age of males when measuring the sword is necessary because males do not initiate sword development until reaching sexual maturity, and the sword continues to grow even after sexual maturity (pers. obs., MRM and ORC; Basolo 1998). For 48 males with swords, sword length was positively related with male size ( $R^2 = 0.74$ ,  $F = 149.4$ ,  $p = 0.0001$ ) and the sword index ranged from 0.32 (male with a standard length of 51.3 mm) to 0.76 (male with a standard length of 51.8 mm), similar to what was recorded for this species by Rauchenberger et al. (1990). Of the eight males under the size of 26 mm, only one did not have a sword, and the sword index for this group ranged from 0.4 to 0.5.

## Discussion

Alternative male mating tactics are often classified based on their relationship to male–male competition (Taborsky 1994, 1997; Mank & Avise 2006a), and yet if strong sexual selection drives the evolution of alternative tactics, males are also selected to circumvent female mate choice. In those cases where mate choice plays an important role, the

alternative tactics should also be evaluated in relation to whether or not they function to coax or coerce females to mate. Males of the northern mountain swordtail (*X. nezahualcoyotl*) range in size from 26 to 50 mm, and all males, regardless of size, possess two morphological traits that are likely to coax females to mate (the sword and expression of the pigment pattern, vertical bars). While the role of the sword in *X. nezahualcoyotl* has not been examined, females prefer males with vertical bars (Morris et al. 2007). The mating behaviors in *X. nezahualcoyotl* ranged from coaxing (headstands, frontal display) to more coercive (backing, fast chases). Larger males were more likely to use coaxing behaviors, and small males were more likely to use coercive behaviors in both the laboratory and the field. In addition, the largest males never used the most coercive behavior in the laboratory setting, even in the context of a larger competitor, and the small males never using the most coaxing behavior, even when alone with females.

Conditional alternative mating strategies are composed of tactics that are not genetically determined, but are condition-dependent (Gross 1996). Therefore, as the range of behaviors the largest and smallest males used did not change when alone with females as compared to in the presence of a larger competitor, one might argue that the large and small males in this species represent different alternative mating strategies (sensu Gross 1996). There are at least two arguments against this conclusion, however. First, even though as in other poeciliids, male size in *X. nezahualcoyotl* is influenced by *P*-alleles on the Y chromosome, there is the potential for overlap in the sizes of males with the two genotypes depending on environment (Kallman 1989). Therefore, to determine if the relationship between male size and the use of different mating behaviors is a direct effect of *P* allele control of size at sexual maturity, when compared with an indirect effect of responding to the conditions of male size, a study similar to the one conducted for *X. multilineatus* (Zimmerer & Kallman 1989) is needed. Zimmerer & Kallman (1989) determined that the use of fast chase in *X. multilineatus* was tightly linked to the 's' allele at the *P* locus and not an indirect effect of male size by comparing males that overlapped in size (largest small 's' males and smallest intermediate 'I' males). Even if the males with the 's' genotype were larger than the 'I' males, 's' males used fast chase while 'I' males did not. Second, we argue that changing the competitive context may not be the best way to expose the full range of behaviors in the case of alternative behav-

iors produced by strong female mate choice. Instead, these behaviors may be more strongly influenced by a given female's preference. If not all females prefer the same males, testing males with a range of females that vary in their preferences would be a better method of determining if the behaviors males use are context-specific. Variation in female preference because of female size has been reported for different preferences in several species of swordtails (Morris et al. 2006; Rios-Cardenas et al. 2007) as well as in guppies (Kodric-Brown & Nicoletto 2001), and we present some evidence to suggest that males may modify the degree to which they interact with a female depending on the size of the female: the number of behaviors a male used in the laboratory study when alone with a female was greater when they were placed with smaller as compared to larger females.

Attempted forced copulations, also known as 'gonopodial thrusts', differ from copulations in which the female cooperates and are a type of forced insemination found throughout poeciliid fish (Farr 1989). Attempted forced copulations result in the females fleeing and an ending of the courtship bout, and therefore, mating behaviors correlated with gonopodial thrusts always occur before the attempted copulation within a bout. Cooperative copulations are rarely observed in the laboratory, and may be rare in general as females can store sperm, producing broods for up to 10 mo after being isolated (Constantz 1984; MRM, ORC, JB unpubl. data). The mating behaviors of *X. nezahualcoyotl* were classified as being more coercive or coaxing based on the correlation of the mating behavior with attempted forced copulations. Zimmerer & Kallman (1989) made a similar observation concerning the various behaviors used by the 's' males in *X. multilineatus*, and ranked frontal displays as being the least likely to be followed by an attempted forced copulation, followed by circling behavior, and then fast chase (*X. multilineatus* does not use headstands). Of the mating behaviors we scored in *X. nezahualcoyotl*, we ranked headstand as the least likely to be followed by attempted forced copulations, followed by frontal display, backing, and fast chase. We discuss both headstand and backing in more detail below.

The behavior 'headstand' had not been previously described for *Xiphophorus* fishes, but has been observed in at least three other species (*X. cortezi*, Fernandez & Fernandez in press; *X. malinche* and *X. montezumae*, MRM unpubl. data). This behavior is similar to 'head-down posture', which has been

described for several different species of fish, including sticklebacks (Wootton 1976) and smallmouth bass (Ridgway et al. 1989). While it is not clear if this behavior is homologous or has evolved repeatedly in these different groups of fishes, convergent evolution of behaviors in ray-finned fishes appears to be common (Mank & Avise 2006a). In our study, we examined headstand in the context of male-female interactions, but they are also used during male-male competition in *X. nezahualcoyotl* (Lyons & Morris in press). One of the reasons attempted forced copulations are less likely to follow a headstand may be that it would be difficult to initiate a chase or copulation from this position. Larger males may perform more headstands than smaller males if females are less likely to flee from a larger male; therefore, a larger male would be less likely to lose the mating opportunity while performing this behavior than a smaller male. However, as headstands are also used in male-male contests that can be observed by females, the use of this behavior may need to be considered in the context of communication networks and unintended audiences as well (McGregor & Peake 2000).

For smaller, less attractive males, backing behavior may be a safer courtship behavior than headstand. The backing behavior we observed bears resemblance to that described by Haas (1993) as 'arching', in which the male alternates swimming backward and forward while facing away from the female. Haas (1993) noted qualitative differences between species of *Xiphophorus* including *X. nezahualcoyotl* (identified as *X. montezumae*) and observed this behavior in *X. clemenciae*, *X. alvarezii*, *X. helleri*, and *X. signum*, but not *X. nezahualcoyotl*. Zimmerer & Kallman (1989) reported that some male *X. multilineatus* swam backwards toward a female, but this behavior was not common and was scored as part of the frontal displays. Ryan & Causey (1989) also note that some *X. nigrensis* males will back into a parallel swim from the transverse approach. When *X. nezahualcoyotl* males were alone with three females, the rate of backing behavior was positively correlated with attempted forced copulations. Haas (1993) suggested that this behavior is often followed by attempted forced copulations, as the male could continue to move backwards far enough to be alongside the female. Therefore, as it would be difficult to chase a female while swimming backwards, this behavior may be intermediate in the dichotomy between 'coaxing' and 'coercive' mating behaviors, as it still puts the male in a position where attempted copulations are possible.

'Vertical bars' is a pigment pattern (Gordon 1931; Atz 1962) found throughout swordtails and platyfishes (*Xiphophorus*). The bars function as a sexually selected signal that evolved first in the context of female mate preference and later as a signal in male–male competition (Morris et al. 2007). *X. nezahualcoyotl* females preferred vertical bars in a previous study (Morris et al. 2007) while no significant response to the bars was detected in males (Moretz & Morris 2006). In our field study, the same males expressed their bars in the context of interacting with females and interacting with males, and these males had higher rates of dominant behaviors and lower rates of submissive behaviors than males that did not express their bars. These results suggest that there is information about dominance available in bar expression to both males and females, even if the timing of the bar expression was not predictive of biting as in other species (Moretz & Morris 2006). Males that expressed their vertical bars were more likely to use headstands, suggesting that these two behaviors may in some way be linked as part of a more complex display. While females have been shown to prefer males with bars in the laboratory, in our field study we found that males that expressed their bars were on quadrants with fewer females rather than more. It seems unlikely that this result reflects the inability of females to express their preference to associate with barred males in the field because of male–male competition, as males that expressed their bars were also using more dominant behaviors. Instead, females may alter their preference for the bars in the field if predators are present. Such changes in female mate preference when predators are present have been documented for other swordtails (*X. helleri*, Johnson & Basolo 2003). We conclude that the function of vertical bars is at a transitional stage in this species, with bar expression attracting females, possibly only in safe environments, but without enough short-term predictive information about male behavior for males to use as a signal in male–male competition.

Finally, the mating behavior and morphology of small *X. nezahualcoyotl* are not more similar to its closest relative *X. continens* than the three other species of *Xiphophorus* for which this type of data were available. *X. continens* males have not only lost large male size, but appear to have lost the sword and vertical bars as well (Morris et al. 2005), both sexually selected male traits (sword, Basolo 1990, 1996; vertical bars, Morris et al. 2007). This differs significantly from *X. nezahualcoyotl*, as even the smallest *X. nezahualcoyotl* males have a sword and vertical bars. The use of vertical bars by the smallest males in

*X. nezahualcoyotl* males also contrasts with the small males in *X. multilineatus*, which have an autosomal gene that suppresses bar expression (Zimmerer & Kallman 1988). Small *X. nezahualcoyotl* males may have retained the use of vertical bars to attract females because of the bars' limited role in male–male competition in *X. nezahualcoyotl*. As for mating behaviors, *X. continens* used fast chases and a behavior not seen in *X. nezahualcoyotl* (gonoporal nibbling), the latter one recognized as a symplesiomorph by Haas (1993) as it is shared with other poeciliids. While the function of nibbling is unclear, it has been suggested that males use this behavior to determine the reproductive status of the female (Farr & Travis 1986). Therefore, even though typical courtship behaviors used by *Xiphophorus* fishes contain phylogenetic information (Heinrich & Schroder 1986; Haas 1993), the differences in mating behavior and morphology of the small *X. nezahualcoyotl* when compared with those of *X. continens* remain an enigma. The apparent lack of selection on male size through either female mate choice or male–male competition in *X. continens* (Morris et al. 2005) may explain the differences.

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