

“Alternative” mating behavior in the swordtails *Xiphophorus nigrensis* and *Xiphophorus pygmaeus* (Pisces: Poeciliidae)

M.J. Ryan and B.A. Causey*

Department of Zoology, University of Texas, Austin, TX 78712, USA

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Summary. The swordtail *Xiphophorus nigrensis* exhibits three relatively discrete male body-size classes that derive from allelic variation at the Y-linked pituitary (P) locus. Previous studies have shown that larger males have greater relative reproductive success, and that females prefer larger males. We describe the mating behavior utilized by males of each size class during individual encounters with females. Small males rely on “chase” behavior, similar to the alternative mating behavior classified as “sneaker” in small males of other species. Large males court and intermediate-sized males court or chase, depending on their body size. There is a strong correlation between P alleles for small size (*s*) and large size (*L*) with chasing and courting, respectively. The relationship between mating behavior of males of the genotype I is ambiguous. In the closely related species *X. pygmaeus*, males are of size similar to smaller *X. nigrensis* males. Paradoxically, these males do not show the courtship display that typifies larger male *X. nigrensis* and many other species of swordtails, but instead often employ chase behavior identical to the alternative mating behavior in small male *X. nigrensis*. We suggest that historical and genetic constraints, in addition to current selection forces, might be important factors in explaining the existence of alternative mating behavior in *X. pygmaeus*.

1986; fish, Kodric-Brown 1985; frogs, Ryan 1980; birds, Searcy and Marler 1981). This variation is often related to male size, and in many species females prefer to mate with larger males (reviewed in Ryan 1985). A consequence of this female preference can be the abandonment of courtship displays by males of the less-preferred phenotype, which instead adopt an “alternative” mating behavior (Rubenstein 1980; Austad 1984; Cade 1984). Similarly, an advantage of large size in male competition also can result in the evolution of alternative mating behavior by smaller males (e.g., Howard 1978; Dominey 1984).

In many fish there are two forms of mating behavior. One form usually consists of conspicuous, species-specific, stereotyped displays directed toward the female, while the alternative mating behavior depends upon males being less conspicuous and/or forcing copulation with females (e.g., Constanz 1975; Warner et al. 1975; Kodric-Brown 1977, 1986; Wirtz 1978; Gross 1979, 1982, 1984, 1985; Dominey 1980; Warner and Hoffman 1980; Hughes 1985; Farr et al. 1986). There is little evidence for any animals, including fish, that these alternative mating behaviors have evolved, at least in part, as mechanisms to circumvent female preferences. To argue such requires: (1) a correlation between a male phenotypic trait and variance in male mating success in nature; (2) experimental evidence showing that female preference based on this trait contributes to the variance in male mating success; and, (3) documentation that males exhibiting the less-preferred phenotype adopt mating behavior that does not depend on courtship to gain access to females. The first two points have been demonstrated for the swordtail *Xiphophorus nigrensis*. One goal of this study is to determine if the smaller, less-preferred males in this species exhibit some form of alternative mating behavior.

Introduction

Variation among courtship displays can influence male mating success (e.g., butterflies, Watt et al.

* Present address: Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138, USA

Offprint requests to: M.J. Ryan

We will then contrast the behavior of these males to the mating behavior of males of *X. pygmaeus* – an entire species with only small males.

Body size is usually a continuously variable trait which is thought to be under significant environmental control with heritable influences being polygenic (Falconer 1981). However, much of the variation in body size in the genus *Xiphophorus* results from allelic variation of a single gene, the Y-linked pituitary (P) locus; there is no allelic variation at the X-linked P locus (Kallman and Borowsky 1972; Kallman et al. 1973; Kallman 1975, 1983, 1984; Borowsky 1987). These alleles determine when the pituitary-gonadal axis is activated which, through its action on the testes and subsequent secretion of androgens, results in maturation. Since males cease or drastically reduce growth at maturity, earlier maturing males are smaller and later maturing males are larger.

Xiphophorus is widely distributed throughout much of Central America (Rosen 1979). *X. nigrensis* and *X. pygmaeus* are both found in rivers of the Rio Panuco basin which empties near Tampico, Mexico. In the swordtail *X. nigrensis* from the Rio Choy, males possess one of three alleles at the Y-linked P locus, *s*, *I*, or *L*, which results in three phenotypic size classes with little overlap: small (<26 mm standard length (SL)), intermediate (26–31 mm SL) and large (>31 mm SL) (Kallman 1983). *X. nigrensis* has chromosomal sex determination; males are heterogametic. However, there is a single autosomal gene that, when present in the homozygous recessive condition, causes XX individuals to mature as functional males (Kallman 1983). Since the *s* allele is fixed on the X-linked P locus, XX males are small. Small males that are XX and XY can be distinguished; XY males have yellow caudal (Kallman 1983). Both XX and XY males were used in this study and behaved similarly.

Heritability for body size of male *X. nigrensis* is 91% (Kallman 1983; Ryan and Wagner 1987). This high correlation between phenotype and genotype, and the fact that body size is not influenced by a wide range of feeding regimes in the laboratory, indicates that the male's genotype can be predicted with relatively high confidence from his body size. Also, Borowsky (1987) showed that relative to the effect of P alleles, social condition has only a minor effect on adult size in male *X. variatus*, and that altering environmental conditions to decrease growth rates does not change the size at maturation. Of course, inferring genotypes of males that are at the border of two size classes needs to be done cautiously. However, for the ma-

ajority of males body size accurately predicts genotype.

Progeny analysis shows that phenotypically larger males (genotypes *I* and *L*) have greater reproductive success than phenotypically smaller males (genotype *s*). In choice tests, females spent significantly more time interacting with larger males (Ryan and Wagner 1987); in addition, due to greater swimming endurance, larger males might also be better able to gain access to females in fast currents (Ryan 1988).

The closely related *X. pygmaeus* is allopatric with *X. nigrensis* and is found in the nearby Rio Axtla (Rosen 1979). All males in this population near Chimalaco are XY and are small, similar in size to the smaller *X. nigrensis* males (Kallman 1983).

We investigated the mating behavior of male *X. nigrensis* and *X. pygmaeus* of each size class for several reasons. First, in *X. nigrensis* female preference for larger males might have resulted in the evolution of alternative mating behavior in smaller males. Second, if there is alternative mating behavior, we can determine the extent to which mating behavior correlates with genotype. Finally, the existence of only small males in the Chimalaco population of *X. pygmaeus* allows for comparisons of phenotypically and phylogenetically similar males (*X. pygmaeus* and smaller male *X. nigrensis*) in social systems that might (due to large variance in male size) and might not (due to small variance in male size) promote the evolution of alternative mating behavior. This allows us to contrast historical and selectionist arguments for the evolution of behavior.

Materials and methods

We recorded the mating behavior of male *X. nigrensis* and *X. pygmaeus* in individual interactions with conspecific females in order to bias the social situation in the laboratory against eliciting alternative mating behavior. We assume that if males exhibit alternative mating behavior under these conditions, they are even more likely to exhibit it under natural conditions in which they compete with other males (e.g., see Farr et al. 1986; Kodric-Brown 1986). Thus these experiments yield a conservative estimate of the occurrence of alternative mating behavior as a function of size class.

Behavioral analysis

All behavioral interactions were video-taped. The experimental tank was a glass aquarium that measured 30 × 60 × 17 cm (height, length, width) and contained water 21–24 cm deep. Black pebbles covered the floor of the tank and dark fabric was draped across the back to facilitate contrast with the light-colored fish. The tank was illuminated with a 56 cm “cool white” fluorescent tube suspended 26 cm above the back edge

Table 1. Description of mating behavior of female and male *Xiphophorus nigrensis* and *Xiphophorus pygmaeus*

Behavior	Description	Behavior	Description
<i>Female behavior</i>			
Stay	Female remains in previous position.		
Slow retreat	Female swims away from the male slowly.		
Dart	Female swims quickly away from the male, stopping only a few cms away from him.		
Fast retreat	Female swims away from the male at a high speed and continues to do so for a great distance.		
<i>Male behavior</i>			
Fast chase	Male chases female quickly and female usually responds with a fast retreat. The fast chase is usually accompanied by attempted copulation (see below) whenever the male gains a position parallel to the female; unless he maintains this behavior for some appreciable amount of time and the fast chase resumes, the attempted copulation is not scored separately.		
Parallel approach	Male swims closely parallel to the female (as if to attempt copulation) but no other copulatory movements are detectable (cf., attempted copulation). The male approaches the female either from behind or by backing out of the transverse position. This display differs from the parallel position of fast chase because it is maintained as parallel swimming (Fig. 1).		
Attempted copulation	Male performs a parallel approach, which is also accompanied by one of		
		the following: sharp, jerking motions toward the female; tilting of the body with dorsum away from the female and ventral surface nearly contacting female's ventral surface; or swinging of the gonopodium (Fig. 1).	
		Sigmoid display	Male twists body into an "S" configuration and brings gonopodium forward toward his head (Fig. 1).
		Transverse approach	Male swims from a position parallel to the female to a position directly in front of her head (within 1.5 cm) with his body perpendicular to hers, and stops. It appears either to be an incomplete or interrupted sexual display (Fig. 1)
		Sexual display	Male performs a transverse approach, and while he is positioned in front of the female, he curves his body into a "C", wrapping himself around the female's head, and quivers back and forth in front of her. Often the male performs a sexual display, swims a small figure-8, and returns to perform another sexual display facing the opposite direction. A continuous uninterrupted sequence of sexual displays performed in this manner are counted as a single sexual display with the time being taken from the beginning of the first to the end of the last sexual display (Fig. 1).
		Circle	Male swims numerous tight circles around the female.

of the tank, and two 75 W incandescent bulbs in 23 cm diameter aluminum reflector lamps that were placed on each side of the tank. Translucent white paper was taped to the sides of the tank to diffuse light entering the tank. Fish were video-taped with a Panasonic WV 3250 color video camera, a 10.5–84 mm zoom lens, and an Everex portable video recorder.

X. nigrensis used in the experiments were offspring of gravid females collected at the headwaters of the Rio Choy, near Tamuin, San Luis Potosi, Mexico. All were born in the laboratory within two weeks of one another; thus regardless of body size, all males were of similar age. Males and females were raised in large, communal tanks. We analyzed the behavior of ten small, nine intermediate, and ten large males. Four of the small males were XY and six were XX. Since their behavior was similar, data were pooled for analysis. As discussed above, when inferring genotypes from males at the border of two size classes results are interpreted with caution.

Most *X. pygmaeus* were offspring of gravid females collected at the Rio Axtla, near Chimalaco, San Luis Potosi, Mexico, and were of similar age to the *X. nigrensis* males. Males that were not born in the lab were wild-caught. There were no apparent differences in behavior between laboratory-born and wild-

caught males. We analyzed the behavior of ten *X. pygmaeus* males that ranged in size from 23–28 mm SL.

After being measured the male was placed in the experimental tank 24 h prior to video-taping. One hour before taping the female was placed in the tank, isolated from the male by an opaque barrier. Females were selected at random from a large communal tank that contained both sexes. The opaque barrier was then removed, allowing the fish to swim freely through the entire tank. Video-taping began when the fish faced one another from a distance not greater than 10 cm. Fish were video taped for a period of 10 min. Pilot studies revealed that male-female interactions decreased after this time period.

Data analysis

All video tapes were analyzed with an Everex recorder and an Everex CM-141 color video monitor. Depending on the behavior, tapes were analyzed at normal speed, slow speed, or frame-by-frame. Durations for each behavior were determined from an internal clock displayed on the screen. Behavior patterns were described and classified using the descriptions of Hemens (1966) as a reference.

The mean rate of behavior and the duration of each behavior were tabulated as a function of male size. Rates and durations of behavior were compared among size classes using a Kruskal-Wallis analysis of variance. Spearman rank correlations were used to examine relationships between body size and behavior. Alpha levels below 0.05 were considered sufficient to reject the null hypothesis.

Results

Mating behavior as a function of size in X. nigrensis

There was a dichotomy in male mating behavior in *X. nigrensis*. Some males attempted to gain access to females through courting (Table 1; Fig. 1). Typically, a male approached a female from the side with a parallel approach. The female usually exhibited one of two behavior patterns: stay or slow retreat. If she exhibited the latter, the male usually maintained the parallel approach by swimming parallel to her. Eventually, he swam around the front of the female and performed a transverse approach. The transverse approach could, but need not, lead to a sexual display. The transverse approach was a necessary predecessor to a sexual display, and appeared to be a sexual display that never reached completion. This sequence of behavior could be performed several times, not always to completion, before the male moved to the side of the female and performed an attempted copulation. We refer to this general sequence of mating behavior as display behavior or courtship. In general, it contained most elements of stereotyped courtship behavior described for other *Xiphophorus* by Franck (1964, 1968), Hemens (1966), and Heinrich and Schroder (1986).

Another mating behavior in *X. nigrensis* appears similar to the sneak or chase behavior that

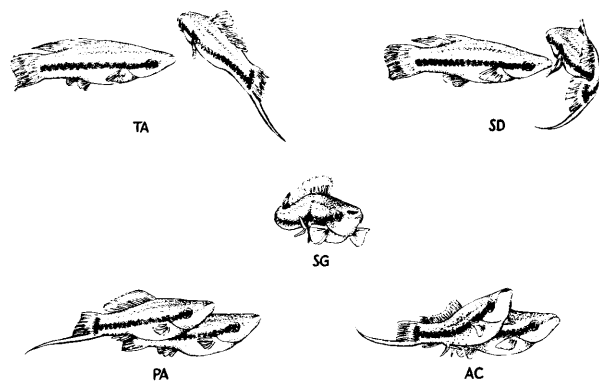


Fig. 1. Mating behaviors of *Xiphophorus nigrensis*: transverse approach (TA), sexual display (SD), sigmoid display (SG), parallel approach (PA), and attempted copulation (AC). See Table 1 for descriptions

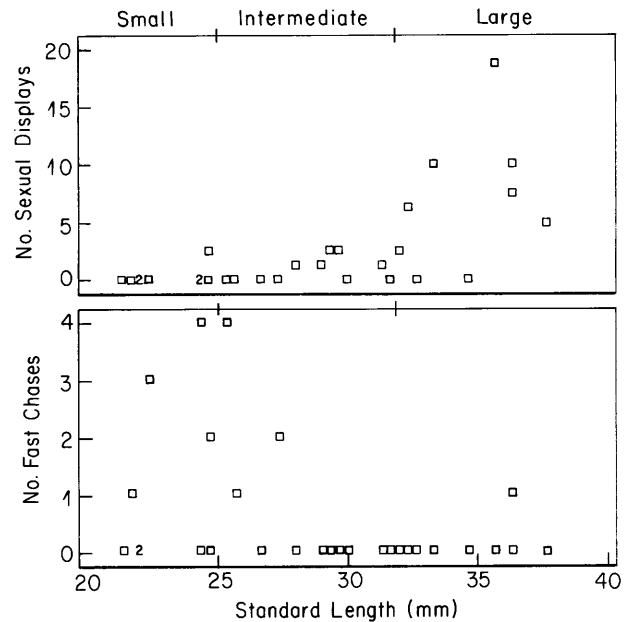


Fig. 2. The number of sexual displays (top) and the number of fast chases (bottom) as a function of standard length. Each box is one datum unless indicated

has been described as alternative mating behavior in other fish (Table 1). A male exhibiting this behavior quickly chased after a female. The female invariably responded with either a dart or, more frequently, a fast retreat. As the male chased her, he attempted to gain position at her side. If he was able to maintain this position the behavior was considered a parallel approach. During this time he repeatedly performed attempted copulations. The apparent dichotomy of courtship display and chase behavior was almost absolute when comparing sexual display and fast chase; only one male exhibited both behavior patterns (Fig. 2).

Size classes were related to the courtship-sneaking dichotomy. Large males exhibited sexual display most frequently, intermediate males were less likely to exhibit sexual display than were large males, and only one small male displayed (Table 2; Fig. 2). These differences among the size classes were statistically significant (Table 2). Male size and frequency of sexual display also were significantly correlated (Spearman rank correlation, $r = 0.70$; $P < 0.01$; Fig. 2). Small males, in contrast, showed a significantly greater frequency and amount of time devoted to fast chase than large males (Table 2; Fig. 2). The differences in the frequency and duration of fast chases were not statistically significant when intermediate males were included in the comparison (Table 2), and there was not a significant correlation between size and fast chase ($r = -0.09$; $P > 0.10$; Fig. 2).

Table 2. The mean (SD) frequency and duration of mating behavior of male *Xiphophorus nigrensis* of each size class. $n=10$ small, 9 intermediate, 10 large. *freq.* frequency, *dur.* duration, *AC* attempted copulation, *PA* parallel approach, *FC* fast chase, *TA* transverse approach, *SD* sexual display, *SG* sigmoid display

Size class	Behavior					
	AC	PA	FC	TA	SD	SG
<i>Small</i>						
\bar{x} freq.	2.4 (2.3)*	3.3 (3.8)	1.4 (1.7)*	0.6 (1.3)	0.2 (0.6)*	0.2 (0.6)*
\bar{x} dur.	6.1 (6.0)*	4.0 (5.7)	3.4 (4.7)*	0.5 (1.3)	0.1 (0.6)*	—
<i>Intermediate</i>						
\bar{x} freq.	0.6 (1.0)*	0.3 (0.7)	0.3 (0.7)	1.1 (1.3)	0.8 (0.8)*	2.6 (2.3)*
\bar{x} dur.	0.7 (1.0)*	0.2 (0.4)	0.3 (0.9)	1.3 (2.0)	1.8 (2.5)*	—
<i>Large</i>						
\bar{x} freq.	1.9 (2.6)*	1.9 (2.6)	0.1 (0.3)*	1.1 (2.1)	5.6 (5.7)*	1.7 (2.9)*
\bar{x} dur.	2.3 (3.9)*	1.8 (2.0)	0.0 (0.2)*	1.5 (2.9)	6.6 (5.8)*	—

* signifies statistically significant differences ($P < 0.05$) using a Kruskal Wallis test

Table 3. The mean (SD) frequency and duration of mating behaviors of male *Xiphophorus pygmaeus*. $n=10$. *AC* attempted copulation, *PA* parallel approach, *FC* fast chase, *TA* transverse approach, *SD* sexual display, *SG* sigmoid display, *C* circle

	Behaviors						
	AC	PA	FC	TA	SD	SG	C
\bar{x} freq.	1.3 (1.3)	4.0 (0.7)	3.3 (2.7)	1.8 (4.7)	0 (0.0)	1.3 (1.9)	—
\bar{x} dur.	1.3 (1.2)	0.3 (0.7)	11.3 (13.0)	—	0 (0.0)	—	6.9 (25.3)

The tendency to express either fast chase or sexual display characterized the small and large size class, respectively, but this was not true of the intermediate size class. This size class was composed of males of each behavioral type; smaller males, which were behaviorally similar to males of the small size class, and larger males, which were similar to males of the large size class. Figure 2 shows that a transition from chasing to courting occurred at 28 mm SL.

The size classes also differed significantly in the frequency and amount of time devoted to attempted copulations (Table 2). Small males showed greater rates of attempted copulation, followed by large and then intermediate males. Small males were much more likely to repeatedly exhibit attempted copulations while swimming along side the female (parallel approach) even though the female was swimming away at fast speeds. It would not be surprising if the rate of successful copulations were higher for large males than for small males, but we were not confident in assigning successful copulations.

The sigmoid display was of short duration, thus only frequency and not time was measured. Size

classes differed significantly in the frequency of sigmoid displays but, unlike any other behavior, these were mostly exhibited by intermediate males (Table 2). This behavior was not common among small males, and is the same behavior described for *X. helleri* by Hemens (1966). The function of this behavior is not clear. Neither the frequency nor the amount of time devoted to transverse approach and parallel approach differed significantly among size classes.

Mating behavior in X. pygmaeus

Male *X. pygmaeus* performed most of the same mating behaviors seen in *X. nigrensis*, with two exceptions. As with small *X. nigrensis* males, the *X. pygmaeus* males did not exhibit the sexual display but instead showed a high frequency of fast chase (Table 3). They also showed a behavior not exhibited by the *X. nigrensis* males that we studied—circling. This was the most frequent mating behavior exhibited by male *X. pygmaeus*. There were no significant correlations between male size and any of the behaviors recorded (Spearman rank correlation, all $r < 0.32$, all $P > 0.05$).

Discussion

Mating behavior in X. nigrensis

Based on the strong correlation between body size and P alleles, progeny analysis suggests that larger *X. nigrensis* males (genotypes *I* and *L*) have greater reproductive success in nature, and female choice tests suggest that some of this size bias in reproductive success is due to female preference for larger males (Ryan and Wagner 1987; see also Zimmerer and Kallman, in press). The first conclusion from our results is that small males, which are at a mating disadvantage due to female preference, rarely court and instead chase females, while males in the large size class, which are at a mating advantage due to female preference, rarely chase and mostly court. Together with data on variance in male mating success and female preference, this strongly suggests that sexual selection by female choice is at least partly responsible for the evolution of the alternative mating behavior of small males in this species, as is predicted (e.g., Rubenstein 1980; Austad 1984; Cade 1984). This alternative mating behavior is similar to that reported in other fish in which large males have a mating advantage due either to female choice or male competition (e.g., Constanz 1975; Warner et al. 1975; Kodric-Brown 1977, 1986; Wirtz 1978; Gross 1979, 1982, 1984, 1985; Dominey 1980; Warner and Hoffman 1980; Hughes 1985; Farr et al. 1986). The fact that small males rarely court but were able to fertilize females both in nature and in the laboratory (Zimmerer and Kallman, in press) suggests that small males are able to gain successful copulations by chasing.

Male-male interactions appear to be less important in the evolution of alternative mating behavior in this species. Preliminary data show that in triads consisting of one female and two males, the mating behavior of small males is the same, whether their male competitors are small or large, and that large males are more aggressive toward other large males than they are to small males. Similarly, in aggressive interaction among males in the absence of females, large males are more aggressive to other large males than to small males. Thus the alternative mating behavior of small males appears to have evolved in response to female preference rather than male-male interactions.

Intermediate males resembled either small or large males in the mating behavior they exhibited; the shift in behavior occurred at 28 mm SL. Thus the second conclusion from this study is that all males generally fall into one of two mating types:

smaller males that chase females and larger males that court. Males of the small and large size class generally fall into only one of the mating types, while males of the intermediate size class can be of either type, depending on their body size.

Our data offer strong evidence that there is a correlation between the two mating types and two of the genotypes. *s* males (both XX and XY) were more likely to chase females while *L* males relied extensively on courtship behavior to gain access to females. We can not reach a firm conclusion regarding the mating behavior of males of genotype *I*. If all males in the intermediate size class were of the *I* genotype, then this genotype encompassed both mating types, with mating behavior being determined by body size variation within the genotype. Alternatively, it is possible that the intermediate-sized males that chased, all of which were within a few mm of the small size class, were actually *s* males. If so, then *s* males primarily chased while *I* and *L* males primarily courted. Unfortunately, there are no known genetic markers that allow discrimination of *s* and *I* genotypes. Also, our data do not allow us to determine if there are genes for the form of mating behavior that are correlated with P alleles (at least *s* and *L*), or if all males have the genetic potential for both forms of mating behavior, and the form of behavior exhibited is determined by the male's body size.

Zimmerer and Kallman (in press) have investigated mating behavior in *X. nigrensis* from the Rio Coy. This population has four P alleles and body size overlaps among allelomorphs. Their results are similar to ours in that they find that small males, but only small males, exhibited fast chase. Their results differ from ours in that small males also exhibited, albeit at a low frequency, sexual display and circle. They suggested that mating behavior has a genetic basis because males of the smaller of the two intermediate size classes did not chase, even if they were smaller than some of the males that bear Y-linked *s* alleles and do chase.

Why do X. pygmaeus lack courtship and large size?

X. pygmaeus males differ from male *X. nigrensis* from the Rio Coy by exhibiting circling behavior, although this behavior was exhibited by small males in the Rio Coy population (Zimmerer and Kallman in press). Whether circle is a courtship display or a behavior that is used to corral the female, allowing the male to gain better access for forced copulation is not clear. Franck (1968) suggested that this behavior is a degenerative form

of courtship display that is derived within *X. pygmaeus*. The existence of this behavior in small Rio Coy *X. nigrensis* complicates an interpretation of the evolutionary history of this behavior.

The range in male body size in *X. pygmaeus* from Chimalaco (ca. 20–28 mm SL) is much less than that of its closest relative *X. nigrensis* (ca. 18–40 mm SL); thus there should be less opportunity for the evolution of size-based differences in mating behavior. In *X. nigrensis*, chasing behavior of small males appears to be an alternative to courtship behavior by larger males. Since *X. pygmaeus* males are more similar in size, the existence of a size-based alternative mating behavior, and chasing in particular, seems unlikely. For example, in several fish species the body size of the male relative to that of his competitors, rather than his absolute size determines his mating behavior (e.g., Farr et al. 1986; Kodric-Brown 1986). However, *X. pygmaeus* males did not exhibit the sexual display, the primary component of the courtship behavior that is exhibited by larger male *X. nigrensis* and many other species of swordtails (Franck 1964, 1968; Heinrich and Schroder 1986). The mating behavior exhibited by *X. pygmaeus* is more similar to the “alternative” chasing behavior of small male *X. nigrensis* than to the courtship behavior of larger males.

The lack of courtship in *X. pygmaeus* is especially interesting since female *X. pygmaeus* prefer courting *X. nigrensis* males to their own non-courting males (Ryan and Wagner 1987). Ryan and Wagner suggested that female preference for courting males is a trait shared by *X. nigrensis* and *X. pygmaeus* through a common ancestor. Thus historical constraints rather than current factors associated with the social system might explain the preference of female *X. pygmaeus* that results in the heterospecific mating preference.

In summary, our studies of the courtship behavior of *X. nigrensis* are consistent with theories of social behavior that predict the expression of alternative mating behavior by males of less-preferred phenotypes. In *X. nigrensis* this behavior is correlated to some extent with genotype (*s* and *L*). Both mating types occur in males of the the intermediate size class but genotype (*s* or *L*) can not be assigned with full confidence to those smaller males of the intermediate size class that chase. The lack of certain courtship behavior patterns and the prevalence of chase behavior in *X. pygmaeus* appear contrary to expectations of social-behavior theory, because chase behavior usually is an alternative to courtship, which does not exist in *X. pygmaeus*. Both phylogenetic and genet-

ic constraints, and the possibility of different selection regimes accounting for the lack of courtship behavior in *X. pygmaeus* relative to *X. nigrensis* might prove important in understanding this paradox.

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