



How female size and male displays influence mate preference in a swordtail

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Building a complete model of animal behaviour requires knowing both the internal and external factors that influence behaviour. As recent genomic and neural studies begin to establish the northern swordtail, *Xiphophorus nigrensis*, as a model for proximate explorations of female mate preference, it is important to recognize the complexity of other factors that can drive variation in female preference. In this study, we determined how different experiential and social factors correlate with interindividual variation in female mate preference: female body size, sexual experience and male behavioural displays. We found a significant positive correlation between female size and female preference for large males, as well as a significant relationship between male activity and female preference. We also demonstrate that copulating at least once may be sufficient to increase preference for large males. Our identification of these relationships emphasizes the multiple and diverse types of mechanisms that can influence variation in female mate preference and encourage their consideration in future studies when trying to assess why and how females choose males.

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Experience and social interactions can influence female mate choice in a variety of taxa (Westneat et al. 2000). As a female sexually matures, her rearing environment can alter her preference function and choosiness of future mates (Walling et al. 2008; Holveck & Riebel 2010; Rutledge et al. 2010; Woodgate et al. 2010; Adkins-Regan 2011). After reaching sexual maturity, however, female mate preferences may continue to be plastic as females gain sexual experience (Kodric-Brown & Nicoletto 2001b; Coleman et al. 2004; Morris et al. 2006; Tudor & Morris 2009; Rebar et al. 2011). Some females make mate choice decisions by utilizing social information from other females by mate choice copying (Schlupp et al. 1994; Dugatkin 1996; Westneat et al. 2000; Godin et al. 2005; Servadio et al. 2009), or by observing sexual displays (Andersson 1994; Kodric-Brown & Nicoletto 2001a; Patricelli et al. 2002; Elias et al. 2006). As such, sexual and social experiences represent potentially important sources of variation in female mate preferences, and knowing their contribution (if any) will give us a more comprehensive view of mate choice mechanisms and their evolutionary consequences for a particular species.

The northern swordtail, *Xiphophorus nigrensis*, represents one of the few species where studies can tractably examine both the proximate and ultimate mechanisms of female mate choice. Studies from our laboratory have identified molecular and hormonal

mechanisms correlated with individual variation of female mate preference (Cummings et al. 2008; Ramsey et al. 2011). Furthermore, a rich history of experimental work has dissected how specific male attributes such as size (Ryan & Wagner 1987; Ryan et al. 1990; Ryan & Rosenthal 2001; Cummings & Mollaghan 2006), sword (Rosenthal et al. 2002) and UV ornamentation (Cummings et al. 2003, 2006) influence female preference response. To gain a complete understanding of the processes driving female mate choice within this species, however, we must explore the influence of the female's experiential state as well as the more dynamic traits (e.g. behaviour) of the male on a female's response. In this study, we explored whether an *X. nigrensis* female's body size (a proxy for age), sexual experience (virgin versus nonvirgin) and male behavioural displays influence variation in mate preference for large males.

Poeciliid fishes (guppies, mollies, platyfish and swordtails) are a popular taxon to examine the evolution of female mate choice (reviewed in: Houde 1997; Ryan & Rosenthal 2001). Although poeciliid females will show, on average, a preference towards particular male phenotypes under certain contexts, there is ample individual variation amongst females, which facilitates identifying underlying mechanisms (Brooks & Endler 2001; Brooks 2002; Cummings & Mollaghan 2006; Morris et al. 2006, 2010). Female *X. nigrensis* have indeterminate growth (Kallman 1989; Morris & Ryan 1990), and the larger classes of males typically court females, while the smallest size class exhibit forced copulation (Ryan & Causey 1989). *Xiphophorus nigrensis* females generally prefer an assortment of secondary sexual characteristics (Ryan &

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Wagner 1987; Ryan et al. 1990; Ryan & Rosenthal 2001; Cummings et al. 2003), and a female's preference for larger males does not significantly vary across her reproductive cycle (Ramsey et al. 2011). Variation in gene expression in the whole brain, specific brain regions and circulating oestradiol levels are significantly correlated with female mate preference (Cummings et al. 2008; Ramsey et al. 2011; R. Y. Wong, M. Ramsey & M. E. Cummings, unpublished data). Understanding how experiential (i.e. female size and sexual experience) and social factors (e.g. male behaviours) contribute to variation in female mate preferences will allow us to build a more complete model for female mate choice behaviour.

METHODS

Female Mate Choice Trials

All experimental procedures were approved by the Institutional Animal Care and Use Committee at the University of Texas at Austin (protocol number 07110101). In total, we observed preference behaviour from 176 sexually mature *X. nigrensis* females. Some females were laboratory reared in sexual isolation ($N = 13$) and others were either wild-caught females or progeny of these females from Nacimiento de Rio Choy in the state of San Luis Potosi, Mexico, from collection trips in 2005, 2006, 2008, 2009 ($N = 163$). We followed established methodology for measuring female preference in a dichotomous choice paradigm (Cummings et al. 2008) and tested each female only once. Females were tested throughout the spring, summer and autumn (February–November) during 2005–2010. As female *X. nigrensis* breed continuously throughout the year (Morris & Ryan 1992), seasonal effects on mate preference are considered negligible. All females were sexually isolated at least 2 weeks before behavioural testing to ensure sexual motivation, which is standard in this system (Morris et al. 1995, 1996; Rosenthal & Evans 1998; Rios-Cardenas et al. 2007). We subjected females to 30 min in an experimental tank with a large versus a small size class male stimulus behind UV transparent barriers. The centre portion of the tank was subdivided into three 24 cm regions: a middle 'neutral' zone with an 'association' zone adjacent to each stimulus. Under lighting conditions found in the wild (Cummings et al. 2003), females were initially placed into the central region of the tank and allowed 5 min for acclimation within an opaque cylinder before starting the trial. We switched the sides of the stimuli halfway through each trial to avoid side bias. We measured

the amount of time in the association zones for all females, total association time (sum of time in both association zones), along with glide displays (a proxy for receptivity, $N = 172$; Liley 1965; Cummings & Mollaghan 2006) and the number of transits into the neutral zone (a proxy for general locomotor activity, $N = 132$) for a subset of these females. We measured preference for the large or small male by four measures: (1) association time (time spent with each male stimulus), (2) association bias (proportional time spent with each stimulus), (3) the strength of preference (Morris et al. 2010) and (4) a preference score (Cummings et al. 2008). We calculated the strength of preference as the absolute difference in association time between males (e.g. strength of preference_{large male} = time_{large} – time_{small}). We determined preference scores as in Cummings et al. (2008), except that in the present study, we calculated scores according to each male stimulus (e.g. preference score_{large male} = association bias_{large male} + $\log((1 + \text{glides displayed towards large male})/(\text{total number of transits}))$). Prior to behaviour trials, we measured the standard length (the length between the tip of the snout to the end of caudal peduncle) of the majority of females ($N = 166$).

Male Behaviour

For a subset of sexually experienced females ($N = 75$), a single observer (P.S.) identified and quantified stereotyped male behaviour patterns from video (see Table 1 for definitions). For previously described male behaviours, we followed original definitions for quantification (Ryan & Causey 1989; Cummings & Gelineau-Kattner 2009). To optimize video resolution, we videotaped and quantified behaviours of male stimuli only when the female was in association zone adjacent to that male. Because we had a limited number of males, some large ($N = 14$) and small ($N = 13$) males were reused for multiple trials.

Statistical Analysis

All statistics were calculated using SPSS v.18 (SPSS, Chicago, IL, U.S.A.). We used a *t* test to assess differences in time spent in the association zones between the male stimuli. We used a Shapiro–Wilk test for normality. The female standard length, association bias_{large male}, glides and transits were not normally distributed even after a log transformation or an arcsine (square root of association bias). Hence, we used Spearman rank correlations to assess relationships

Table 1
Definitions of stereotyped male behaviours in northern swordtails

Male behaviour	Description
Backward float	Male swims backward for half a body length without changing orientation
Bobbing	Male quickly moves his head from side to side, holding his snout against/near glass; head movements are slight but in rapid succession; one bobbing event is a continuous event (range 1–10 s)
Circle swim	Male swims away from the female for about 2 body lengths, then returns to the female; similar to 'glides' in females (Cummings & Mollaghan 2006)
Elongated male wave	Male swims towards the glass moving his head from left to right (arc ca. 0.25 of male's standard length); entire length of the male undulates with the initial head movement; two full cycles of left-and-right motion usually constitute the shortest elongated male wave
Inactivity pause	No propulsive movement by the male for ≥ 5 s
Lateral display	Male turns sideways away from the female for ≥ 1 s, then turns and faces the female; male may either be stationary or slowly drift forward; performed in a series using the same side or both sides alternately, and at close (≤ 1 body length) or moderate (2–3 body lengths) distance (Cummings & Gelineau-Kattner 2009)
Foraging	Sequence of 3 or more feeding attempts near rocks or other objects
Parallel swimming	Male swims parallel to and within 1 body length of the female (Cummings & Gelineau-Kattner 2009)
Sexual display	Quiver displays and C-shape body bends (Ryan & Causey 1989)
Sigmoid display	Male quickly twists his body into S-shape and brings his gonopodium towards his head (Ryan & Causey 1989)
Solo swimming	Movement that is neither orientated towards the female, nor correlated with female movement (Cummings & Gelineau-Kattner 2009)
Sporadic movement	Characterized by a burst of random, fast swimming; multiple bouts possible
Up and down	Male swims up and down towards the female for at least two full cycles (modified from Cummings & Gelineau-Kattner 2009)

between female standard length and preference score, strength of preference, association bias, glides and transits. To assess the effect of sexual experience on the strength of preference, we used a general linear model (GLM) with female standard length as a covariate. To account for multiple hypotheses testing, we only report significant values after a Benjamini–Hochberg correction (Benjamini et al. 2001).

To analyse the effect of male behaviours on female preference, we used a generalized estimating equation (GEE) and controlled for male size class and female standard length. We used a GEE for repeated measures of the female's preference (strength of preference and preference score; a measure of preference was calculated for both large and small males, see description above). Although all behavioural displays, with the exception of foraging, were shown by at least two males in each size class, behavioural displays shown by fewer than four males in each size class were considered rare across males and were not statistically analysed (parallel swimming, sigmoid display, sporadic movement, foraging, inactivity pause). We calculated total male activity as the sum of the behaviours that were included in statistical analyses. Because of low power, we were not able to reliably account for effects of individual males in our models. For our two main measures of preference (strength of preference and preference score), we ran two GEE models with male size class as a cofactor and female standard length as a covariate that consisted of either the measure of preference and individual male behaviours, or the measure of preference and total activity of the male (sum of all behavioural displays). Significant interaction effects are reported relative to the small male size class. To compare number of individual behavioural displays between large and small males, we averaged the number of behavioural displays for each male and then assessed the difference in the number of displays using a Mann–Whitney *U* test.

RESULTS

Female Mate Preference and Female Size

There were highly significant positive relationships between female size (standard length) and the three measures of preference towards the large male class stimulus: the preference score_{large male} (Spearman rank correlation: $r_S = 0.364$, $N = 123$, $P = 3.5 \times 10^{-5}$; Fig. 1), strength of preference_{large male} ($r_S = 0.44$, $N = 168$, $P = 2.3 \times 10^{-9}$) and association bias_{large male} ($r_S = 0.454$, $N = 168$, $P = 1.4 \times 10^{-10}$). There were no significant correlations between female size and total glides ($r_S = -0.027$, $N = 164$, $P = 0.728$) or transits ($r_S = -0.128$, $N = 123$, $P = 0.157$). There was also

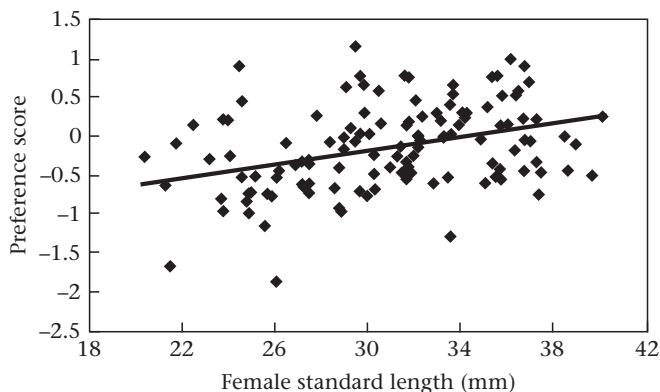


Figure 1. Relationship between female size and preference score towards large males in northern swordtails, *Xiphophorus nigrensis*.

no significant correlation between female size and total association time ($r_S = -0.105$, $N = 168$, $P = 0.177$). Strength of preference_{large male} and preference score_{large male} were significantly and positively correlated with each other (Pearson correlation: $r_{120} = 0.68$, $P = 7.77 \times 10^{-18}$). Association bias_{large male} was significantly correlated with both strength of preference_{large male} ($r_S = 0.958$, $N = 176$, $P = 2.66 \times 10^{-96}$) and preference score_{large male} ($r_S = 0.686$, $N = 131$, $P = 1.44 \times 10^{-19}$). Preference score_{large male} was also significantly and positively correlated with the total number of glides ($r_S = 0.45$, $N = 131$, $P = 6.8 \times 10^{-8}$) and negatively correlated with the number of transits ($r_S = -0.233$, $N = 131$, $P = 0.007$), whereas strength of preference_{large male} was positively correlated only with total glides ($r_S = 0.19$, $N = 172$, $P = 0.01$). There was no correlation between association bias_{large male} and total glides ($r_S = 0.118$, $N = 172$, $P = 0.124$) or number of transits ($r_S = -0.146$, $N = 131$, $P = 0.095$).

Female Mate Preference and Sexual Experience

As expected, sexually experienced females spent significantly more time next to the large male relative to the small male (paired *t* test: $t_{162} = 11.51$, $N = 163$, $P = 8.54 \times 10^{-23}$; Fig. 2a). Virgins, however, showed no significant difference in time spent between the males (paired *t* test: $t_{12} = 1.01$, $N = 13$, $P = 0.33$; Fig. 2b). As virgin females were significantly smaller than sexually experienced females (independent samples *t* test: $t_{166} = 1.99$, $N_1 = 155$, $N_2 = 13$, $P = 0.047$), we did not observe a significant effect of preference for the large males between sexually experienced and virgin females when controlling for female size (GLM: $F_{1, 166} = 1.606$, $P = 0.2$).

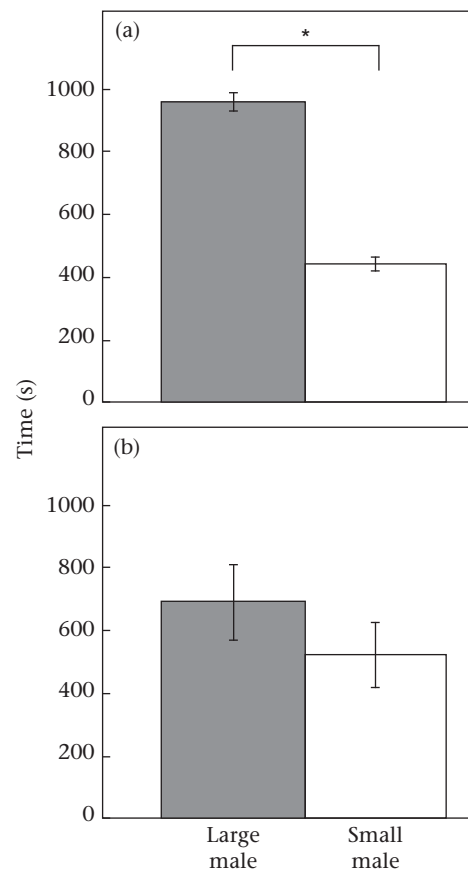


Figure 2. Time spent with large and small size class males by (a) sexually experienced and (b) virgin female swordtails, *Xiphophorus nigrensis*. * $P < 0.001$.

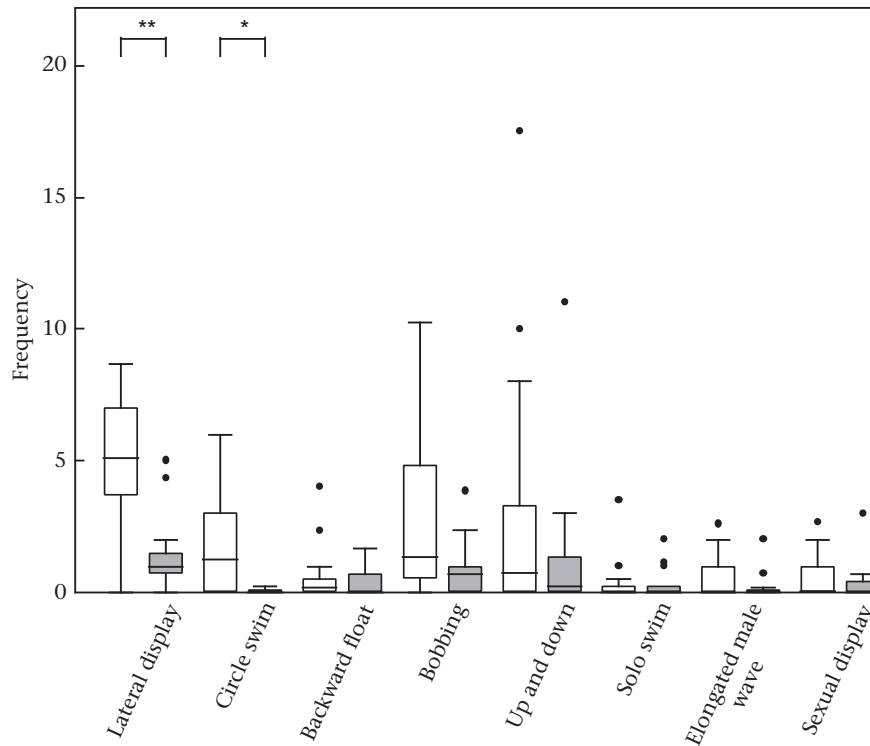


Figure 3. Box plots of the frequency of male behaviours in northern swordtails, *Xiphophorus nigrensis*. □: large males; ■: small males. Lines within boxes represent the medians; whiskers represent maximum and minimum values. * $P < 0.05$; ** $P < 0.001$.

Female Mate Preference and Male Behaviour

Of all the male behaviours, large males performed lateral displays (Mann–Whitney U test: $U = 22.5$, $N_1 = 14$, $N_2 = 13$, $P = 0.0004$) and circle swims ($U = 51$, $N_1 = 14$, $N_2 = 13$, $P = 0.033$) significantly more than small males, but circle swims did not pass a multiple hypothesis correction (Fig. 3). As expected, there was a significant main effect of male size class on female's strength of preference and preference score (strength of preference: general estimating equation, Wald chi-square, $\chi^2_1 = 96.426$, $P < 1 \times 10^{-19}$; preference score: $\chi^2_1 = 49.072$, $P = 2.4 \times 10^{-12}$). One male behaviour ('up and down' display) showed a significant main effect with both measures of preference (Table 2). There was also a significant interaction effect between male size class and up and down displays for strength of preference (Table 2, Fig. 4c). Circle swims and solo swims had significant main effects with the female strength of preference (Table 2, Fig. 4a, b). There were significant interaction effects of elongated male wave with preference score, and of circle swim, bobbing and solo swims with strength of preference (Table 2). There was no significant main effect ($\chi^2_1 = 0.475$, $P = 0.491$) and no interaction effects ($\chi^2_1 = 0.035$,

$P = 0.851$) of total male activity and preference score, or sexual displays and preference score (main effect: $\chi^2_1 = 0.245$, $P = 0.621$; interaction effect: $\chi^2_1 = 0.783$, $P = 0.376$). There were, however, significant main ($\chi^2_1 = 9.942$, $P = 0.001$) and interaction ($\chi^2_1 = 4.801$, $P = 0.028$) effects of total male activity with strength of preference (Fig. 4d), but not between sexual displays and strength of preference (main effect: $\chi^2_1 = 1.117$, $P = 0.291$; interaction effect: $\chi^2_1 = 0.592$, $P = 0.442$).

DISCUSSION

Female experience and male behavioural displays influence female response towards males in *X. nigrensis*. In this species, females of larger size (and presumably greater age and experience) show stronger preference for larger males (Fig. 1). Male behaviours, some of which may indicate a male's motivation or vigour in these experimental conditions (e.g. up–down movements and total activity), can also strongly predict female response. These results suggest that preference behaviour is not hardwired in this species, but rather is moulded over a female's lifetime and can be modulated by specific male behaviours.

Table 2

Significant effects of male behaviour on the strength of preference and preference scores (in parentheses) of female swordtails, *Xiphophorus nigrensis*

Male behaviour	B (mean \pm SE)	χ^2	P
Circle swim	-234.968 ± 61.49	14.601	1.0×10^{-4}
Up and down	56.062 ± 14.113 (0.037 \pm 0.0157)	15.78 (5.71)	7.1×10^{-5} (0.016)
Solo swim	259.096 ± 55.342	21.918	2.8×10^{-6}
Large male*circle swim	250.119 ± 62.144	16.199	5.7×10^{-5}
Large male*bobbing	-32.884 ± 16.219	4.111	0.042
Large male*solo swimming	-199.57 ± 72.806	7.514	0.006
(Large male*elongated male wave)	(0.121 \pm 0.0552)	(4.83)	(0.028)

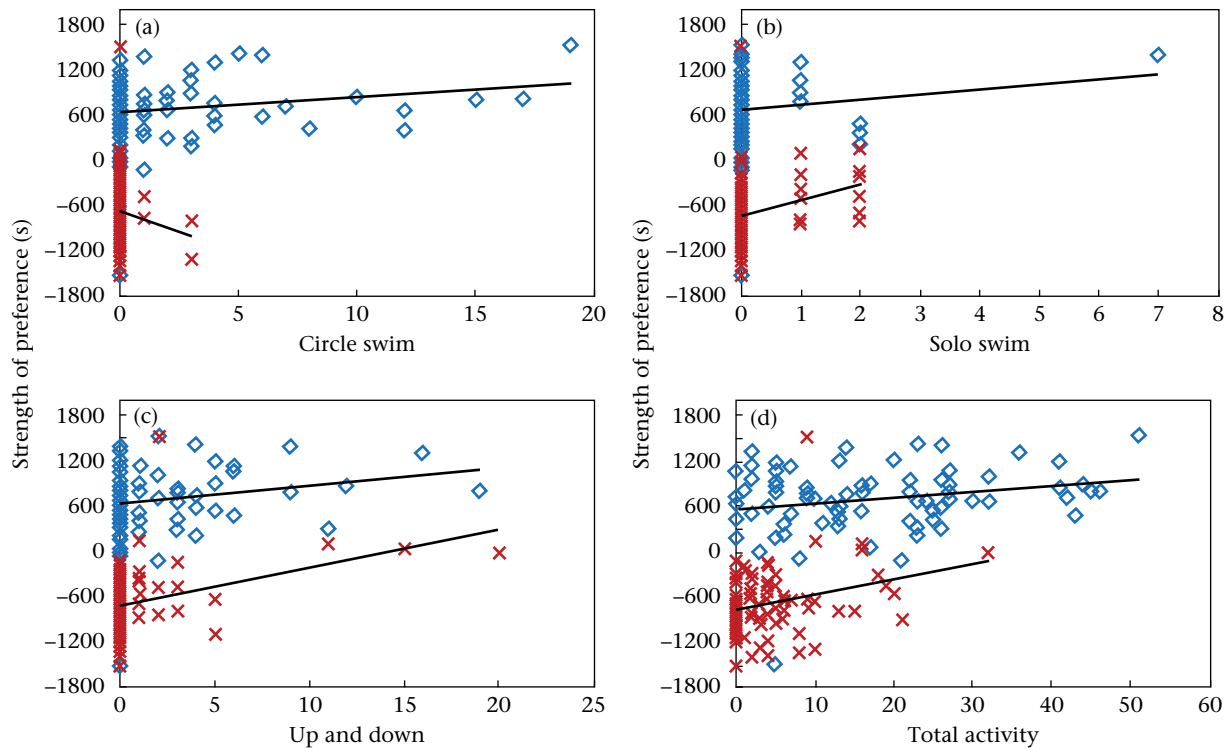


Figure 4. Significant main effect and interaction effects between female strength of preference in northern swordtails, *Xiphophorus nigrensis*, and male behavioural displays: (a) circle swim, (b) solo swim, (c) up and down and (d) total activity. \diamond : displays by large males; \times : displays by small males.

A female swordtail's size can be taken as a proxy of her age (Morris & Ryan 1990; Morris et al. 2006) and may represent her amount of social and sexual experience. In this study, the size of a female *X. nigrensis* significantly predicted her strength of preference, her association bias and her preference score for large males. This is consistent with results for a sister species, *X. multilineatus* (Rios-Cardenas et al. 2007; Morris et al. 2010). Although many interpretations of the observation are possible, we will focus on two with support from data in this study: size-assortative preferences and age/sexual experience. Assortative mating preferences are widely documented across taxa where females can prefer to mate with males of similar size/body shape or coloration (Nagel & Schluter 1998; McKinnon et al. 2004; Salzburger et al. 2006; Elmer et al. 2009; Schluter 2009). In our study, there was a significant positive relationship between female size and the proportion of time she spent with a large male (association bias_{large male}), but there was no significant correlation between female size and total association time. This suggests that motivation does not vary with age, but discrimination between male size classes does. Specifically, larger females tended to spend more time associating with large males, while smaller females showed little discrimination. While small males gain some reproductive advantage by sexually maturing earlier than large males (Morris & Ryan 1990; Ryan et al. 1992), if smaller females do not actively discriminate against them, this may suggest that small males may gain much of their mating success with smaller females. This possibility of smaller *X. nigrensis* females displaying greater tolerance to the small force-copulating males may contribute to the maintenance of alternative mating strategies in this system and its sister taxa, *X. multilineatus* (Morris et al. 2010).

The role of age and sexual and social experience on female preference functions or choosiness is documented across a wide range of taxa from crickets (Rebar et al. 2011) to guppies (Kodric-Brown & Nicoletto 2001b) to birds (Coleman et al. 2004).

Some mechanisms that allow females to modify or refine preferences through time are physiological changes associated with copulation, learning and remembering which males are best (e.g. male–male competition), or copying choices of other females (Schlupp et al. 1994; Rosenqvist & Houde 1997; Westneat et al. 2000; Kodric-Brown & Nicoletto 2001b; Wong & Candolin 2005; Bailey & Zuk 2008, 2009; Servedio et al. 2009; Tudor & Morris 2009). In the present study, smaller (i.e. presumably younger and less experienced) females did not display a strong preference towards large males, whereas larger (i.e. presumably older and more experienced) did (Fig. 1). In *X. nigrensis*, females may refine their preference for larger males with age through learning and memory of male quality or copulation. Whether this learning is based on aspects of reward via mating events with large males, or whether it is driven by aversive learning from negative interactions with small, harassing males is not known.

Shaping of female preferences by sexual and social experience is common across poeciliids (Breden et al. 1995; Marler et al. 1997; Kodric-Brown & Nicoletto 2001b; Walling et al. 2007, 2008; Tudor & Morris 2009). In the congener, *X. malinche*, copulating at least once appears to be sufficient to alter female preference for vertical bar symmetry (Morris et al. 2006; Tudor & Morris 2009). In *X. nigrensis*, a similar scenario may be occurring, as virgin females in our study showed no significant difference in time spent with large or small males, whereas sexually experienced females showed a clear preference for large males (Fig. 2a, b). Although this difference may be due to virgins being smaller than experienced females, with a small number of virgins tested in this study, we had low power to detect a difference. It is interesting to consider whether male behaviour, and perhaps male preference for larger females, influenced the apparent low preference for large males by smaller females. The body size of a poeciliid female is highly correlated with her fecundity (Morris & Ryan 1992; Herdman et al. 2004; Ojanguren & Magurran 2004), and in many species, including

other poeciliids, males prefer to mate with larger and more fecund females (Andersson 1994; Herdman et al. 2004; Plath et al. 2006; Liao & Lu 2009). Thus, it is conceivable that large males in our study also displayed differentially towards larger females. Our statistical analysis did not allow us to evaluate this question, but a more direct examination of how male behaviour differs by female size in this species would be enlightening.

Behavioural displays by the male (e.g. courtship) influencing female preferences are widely documented (Andersson 1994; Kodric-Brown & Nicoletto 2001a; Patricelli et al. 2002; Elias et al. 2006). The interaction between behavioural displays and physical attributes (e.g. size of ornamentation or coloration) can lead to different levels of choosiness depending on the combination of traits (Kodric-Brown & Nicoletto 2001a; Patricelli et al. 2002; Cummings et al. 2006). For example, in guppies, there appears to be a synergistic effect of male courtship display rates and coloration on female preference (Kodric-Brown & Nicoletto 2001a). Similarly, male UV ornamentation and male behavioural activity affect female preference in swordtails, where females prefer large, UV-ornamented males with lower total behavioural activity levels relative to non-UV-ornamented males with higher total activity levels (Cummings et al. 2006). In the current study, we also found a significant effect of total male activity (sum of all behavioural displays; Fig. 4d) and strength of preference. Females tended to spend more time associating with males (e.g. higher strength of preference) that were more active overall (Fig. 4d). Note that although small males benefited more than large males from increased activity, large males garnered much higher female preference responses even in the absence of activity (Fig. 4d).

While a male's total activity was positively related to the strength of preference, only one male behaviour (up and down display) significantly explained variation in female strength of preference and preference score (Table 2, Fig. 4c). Up and down displays could be interpreted as motivation for the male to gain access to the female, by swimming vigorously against the barrier and causing an up and down motion. This behaviour may be attractive to females because it may be a direct indicator of a male's vigour and/or it indicates a male's level of interest in the female. Note that the lateral display, which is a passive display that allows for viewing of ornamentation with little physical activity, was the most frequently displayed male behaviour (Fig. 3), but it had no significant effect on female preference. This suggests that females are more responsive to male displays that are more vigorous (e.g. up and down; circle swim, total activity; Fig. 4). It is surprising that there was no significant main effect of male sexual display on female preference. However, given that full expression of a male sexual display in swordtails requires close contact with the female, we cannot rule out that some of our results were artefacts of the laboratory testing environment. Studying free-ranging behavioural interactions between the sexes and the resulting chances of copulation either in the laboratory (e.g. Ryan & Causey 1989; Cummings & Mollaghan 2006) or in the wild will help elucidate the biological relevance.

There can be many factors that contribute to individual variation in female mate choice. In poeciliids, ecological and social environments, female condition, age, experience, male physical and behavioural phenotypes, gene expression and hormones are just some of the factors that may affect female mate choice. In this study we provided evidence that female size and some male behaviours correlate with female preference. These factors can allow us to build a more complete model of female mate choice and its effects on male behavioural or phenotypic trait evolution in *X. nigrensis*. In this species, females may vary their preferences in response to extrinsic factors such as male secondary sexual characteristics (e.g. body size, UV ornamentation), male behavioural displays, and in

response to intrinsic factors like size (e.g. age/experience) and physiological cues (e.g. regulation of gene expression and hormones). It is likely that combinations of these mechanisms help to shape differences in choosiness across females and even within females across time both in this species and others.

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