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Frequencies of alternative mating strategies influence female mate preference in the swordtail *Xiphophorus multilineatus*

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While studies demonstrating variation in female mating preferences are increasing, we still know very little about the factors that contribute to this variation, and we are therefore unable to predict how selection on males will vary due to female preference. A previous study of *Xiphophorus multilineatus* detected variation in female mate preference, where smaller females had a weaker strength of preference for males that court (courters) as compared to small males that use sneak-chase behaviour (sneakers). We tested the hypothesis that female experience with biased frequencies of courter and sneaker males would result in negative frequency-dependent selection on these male alternative mating strategies through female mate choice. We examined the preferences of naïve females, females given experience with different frequencies of courter/sneaker males in laboratory mesocosm treatments, and wild-caught females collected when the frequencies of males were sneaker biased and equal. The frequency of courter to sneaker males experienced in the laboratory significantly influenced female preference for courter males, but not in the direction we predicted for one end of the frequency distribution: the weakest strength of preference for courter males was from the treatment where courter males were less frequent. The pattern detected in wild-caught females was similar to the pattern detected in the laboratory-mated females, and together they suggest that when frequencies are biased towards either type of male, smaller females have a weaker preference for courter males.

Recent studies of sexual selection have highlighted the importance of environmental changes over space and time on the direction, mode and strength of sexual selection (Jennions & Petrie 1997; Qvarnström et al. 2000; Chaine & Lyon 2008; Lehtonen et al. 2010; Cornwallis & Uller 2010; Svensson et al. 2010). Variation in female mate preference (Qvarnström et al. 2000; Chaine & Lyon 2008; Lehtonen et al. 2010) can contribute to these fluctuations in sexual selection. Variation in female mate preference has been suggested to impact the evolution of male traits by dampening selection on individual male traits (i.e. maintain genetic variation; Chaine & Lyon 2008), maintaining multiple male traits (Coleman et al. 2004), and even leading to species divergence (Svensson et al. 2010). We were interested in the potential for female mate preference to produce negative frequency-dependent selection on male alternative mating strategies, which would help maintain this type of variation across males. Female mate preferences can be altered by social context (Jirotkul 1999; Hebets 2003; Ophir & Galef 2004; Royle et al. 2008; Lehtonen & Lindström 2009; Tudor & Morris 2009; Svensson et al. 2010), which could result in a feedback dynamic producing frequency-dependent selection. For example, in Japanese quail, *Coturnix japonica*, sexually experienced females choose less dominate males after eavesdropping on aggressive male–male interactions where virgin females prefer dominant males (Ophir & Galef 2004). In addition, mate preferences could produce negative frequency-dependent selection if the rare male phenotype is the most preferred (Hughes et al. 1999; Eakley & Houde 2004; see also Kokko et al. 2007).

Theoretical models have suggested that long-term fluctuations in female mate preference may be caused by factors such as density-dependent costs of choice or environmental changes (Houle & Kondrashov 2002). Plasticity in female mate preference allows females to be more selective in environments where there are greater benefits or lower costs to being choosy. Even when female preference is under selection due to the genetic benefits females gain from mate choice, the benefits of being choosy can be context dependent (Qvarnström 2001). Females might be expected to evolve plastic mate preferences in these situations depending on the fitness costs of making a bad decision, the costs to plasticity, and temporal or spatial fluctuations in contexts and dispersal patterns (Qvarnström 2001). Because selection will differ across

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constant as compared to variable environments (Schlichting & Pigliucci 1998; Lenormand et al. 2009), a better understanding of not only how female preference varies, but also the factors that are driving variation in female preference will improve our understanding of selection on male traits as well as the evolution of female mate preferences.

We examined variation in female preference for males with alternative reproductive strategies within the swordtail *Xiphophorus multilineatus*. Four different size classes of males have been identified in this species (Zimmer & Kallman 1989; Kallman 1989); males from the three largest size classes use courtship exclusively, while males from the smallest size class use courtship and a coercive sneak-chase mating behaviour (Zimmer & Kallman 1989). Variation in copy number of *mc4r* genes on the Y chromosome underlies the polymorphism in male size (Lampert et al. 2010), and it is expected that the small male genotypes in this system could have equal fitness with the larger male genotypes by reaching sexual maturity sooner (Ryan et al. 1992; Bono et al. 2011). Frequency-dependent selection, which can maintain genetic polymorphisms within a population (Slatkin 1978), has not been demonstrated for this system. On average, females prefer the larger courter males; however, there is a relationship between strength of preference for courters and female size such that smaller females have a weaker preference (Rios-Cardenas et al. 2007). It has been hypothesized that variation in the strength of female mate preference for the larger courter males could help maintain the two strategies in this species through spatially or temporally oscillating selection (Rios-Cardenas et al. 2007). Smaller females show a weaker preference for large courting males, and, average female size is correlated with the frequency of courter males both across and within populations over time (Rios-Cardenas et al. 2007). Therefore, it was suggested that variation in preference could maintain both male strategies without negative frequency dependence if there was gene flow between populations and/or variation in female size (and thus preference) over time. However, it is not known what factors influence variation in strength of preference based on female size, or whether the variation in preference itself would result in negative-frequency dependent selection.

In this study, we examined the potential for variation in female mate preference in *X. multilineatus* to help maintain these two morphs by producing negative-frequency dependent selection. In nature, fluctuations of courter and sneaker frequencies range from being courter biased to being sneaker biased, and these fluctuations can occur within a generation (Rios-Cardenas et al. 2007). If the strength of preference for the courter males is influenced by the frequency of the courters in a population, such that the strength of preference increases when courters are rare and decreases when courters are common, then female mate preference could be producing negative-frequency dependent selection on the two types of males. We examined this hypothesis by giving females experience with different frequencies of courter and sneaker males in laboratory mesocosms, and by comparing the preferences of wild-caught females collected when the frequency of the two types of males were equal as well as when it was highly skewed towards sneakers.

GENERAL METHODS

The swordtail *X. multilineatus* is a livebearing fish that is found in the Río Coy drainage in the state of San Luis Potosi, Mexico. For female preference experiments, we collected female subjects from Río Oxitipa and we collected stimulus males from Río Oxitipa and Río Tambaque. All fish were fed to satiation daily with Tetramin flakes (Tetra Holdings, Inc., Blacksburg, VA, U.S.A.) and maintained on a 12:12 h light:dark photoperiod at a constant room temperature of 22 °C.

Preference Tests

We assessed female mating preference for courter males as compared to sneaker males by recording association times using standard dichotomous preference tests. Association time in female mate preference tests is a good predictor of the male *X. multilineatus* that females mate with in the field (Morris et al. 2010). Before the tests, we measured standard length of all fish without anaesthetizing them. We isolated all individuals into 18.9-litre aquaria. All females were tested with two different pairs of males, which mitigated the problem of one or more males having some trait in addition to male size that would have some strong influence on female preference, and it provided for a better estimate of each female's preference for courter males. Females were isolated 7–15 days before being tested (except for females from the Río Oxitipa collected in March 2009, which were isolated from 3 to 5 months) and remained isolated 7–14 days between the two preference tests.

Preference tests were carried out in a 208.2-litre rectangular aquarium ($422.6 \times 32.4 \times 53.3$ cm, $L \times W \times H$) divided into five equal sections ($84.5 \times 32.4 \times 53.3$ cm), with the two outermost sections separated from the inner three sections by glass partitions. The inner three sections of the preference aquarium were indicated only by lines on the tank. We placed one male of each pair in each of the outermost sections of the preference test aquarium. The female was placed in the middle section (neutral zone) inside a clear holding tube. We allowed both males and females to acclimate for 10 min before releasing the female. We made observations behind a sheet of Plexiglas covered with one-way vision film. We recorded the time that females spent in the inner two sections adjacent to each male (choice zone) for a 10 min period (trial period). We switched the placement of the males between the first and second trials to control for potential side biases of females. The time interval between the first and second trials included the transfer time plus the 10 min acclimation. Tests where the female did not spend some time on both sides of the aquarium across the two trials were considered to be side biased and were repeated at least 7 days after the side-biased test. Only data from the repeated test was included in the analysis; no females were excluded from the analyses due to side-biased tests; thus, all females had two non-side-biased tests.

Virgin Females (Experiment 1)

Wild-caught females (collected in April 2006) were isolated into 18.9-litre aquaria and all fry dropped were placed into a 208.2-litre communal aquarium. The communal aquarium was checked once per week, and male offspring were removed once they started to develop a gonopodium. Female offspring were also removed once they reached sexual maturity (indicated by the formation of a brood spot; Meffe & Snelson 1989; Morris & Ryan 1992) and placed into a 208.2-litre all-female communal aquarium that was visually isolated from males until testing occurred.

We tested 18 females that had no mating experience (virgin females; mean ± SE size: 27.8 ± 0.5 mm, range 24.1–31.7 mm) for their preference for courter males as compared to sneaker males. We used a total of 14 courter males and 12 sneaker males to form 36 unique male pairs (males were not placed into more than five pairs and no pair was used twice) as stimuli. A prior study using this method of creating male stimulus pairs demonstrated that female preference in the laboratory is statistically correlated with that in the field (Morris et al. 2010). Mean size ± SE of courter males was 36.9 ± 0.4 mm (range 33.6–39.8 mm) and that of the sneaker males was 23.8 ± 0.4 mm (range 21.2–25.8 mm). The mean size difference between males within a pair was 12.8 ± 0.4 mm (range 7.4–15.6 mm).

Preferences of Experienced Females (Experiment 2)

We examined the role of experience with different frequencies of courter males to sneaker males in a laboratory setting (stocked mesocosms) and in the field (we sampled females when the frequency was sneaker biased and equal). Wild-caught females (collected from the Río Oxitipa in January 2007) were isolated into 18.9-litre aquaria and fry were housed in 18.9-litre aquaria in groups of six or less. Virgin females were obtained and housed with the methodology described above.

Virgin females were randomly assigned to three treatment groups and placed into the 90-litre treatment tanks. The treatments were sneaker biased (one courter male and five sneaker males; 1C:5S), equal (3C:3S) or courter biased (5C:1S). These frequencies are similar to those detected in nature (Rios-Cardenas et al. 2007). There were three replicates for each treatment group for a total of nine treatment tanks. Females remained in the treatment tanks for 20 days gaining mating experience prior to testing. Each treatment tank housed six females and six males; thus, we tested a total of 54 females (18 females per treatment). There was no difference in female size among treatment groups (mean ± SE size: 1C:5S treatment = 28.1 ± 0.5 mm, range 23.2–31.9 mm; 3C:3S treatment = 28.1 ± 0.5 mm, range 23.4–31.6 mm; 5C:1S treatment = 28.2 ± 0.5 mm, range 23.2–30.7 mm; ANOVA: $F_{2,53} = 0.013$, $P = 0.987$).

Females were individually isolated once they were removed from the treatment tanks and tested for their mating preferences (see General Methods above). We used a total of nine courter males and nine sneaker males to form 81 unique male pairs to be used as stimuli across all three treatments. Thirty-eight pairs were used twice with different females. The mean size ± SE of the courters was 37.6 ± 0.6 mm (range 34.7–39.9 mm) and that of the sneakers was 24.2 ± 0.5 mm (range 22.3–26.4 mm). The mean size difference between males within a pair was 13.2 ± 0.2 mm (range 8.3–17.4 mm).

The frequency of sneaker males to courter males in the Río Oxitipa in January 2007 was sneaker biased (3C:19S). Wild-caught females collected at this time had a strong preference for courter males (mean time with courter males ± SE = 1442.9 ± 43.97 s; mean time with sneaker males = 707.3 ± 45.11 s; paired t test: $t_{34} = 8.7$, $P < 0.001$; Morris et al. 2010). In the current study, we tested the preference of wild-caught females collected in March 2009 from the Río Oxitipa, when the frequency of courters to sneakers was more or less equal (18C:14S). For wild-caught females, we assumed that the ratio of courters to sneakers measured at the time that the females were collected approximated the relevant ratio experienced by females. Twenty-three adult females (mean ± SE size: 25.39 ± 2.9 mm, range 22.8–31.9 mm) were brought back to the laboratory, housed in individual 18.9-litre tanks and tested for their preference for courter males as compared to sneaker males. Four females were retested once due to side biases. We used a total of 13 courter males and 13 sneaker males to form 46 unique male pairs (males were not placed into more than 8 pairs) to be used as stimuli. Mean size ± SE of courter males was 29.7 ± 3.54 mm (range 23.2–35.2 mm) and that of the sneaker males was 21.3 ± 1.10 mm (range 19.38–23.34 mm). The mean size difference between males within a pair was 7.4 ± 2.32 mm (range 3.1–12.2 mm).

Statistical Analysis

For each experiment, we determined whether females showed a significant preference for courter males by comparing the total time (summed across the two tests) they spent with the courter male to the total time they spent with the sneaker male using paired t tests. We calculated the average strength of preference for courter males for each female. We calculated strength of preference for courter males for each of the two tests by subtracting the time spent with the sneaker male from the time spent with the courter male. We then averaged the strength of preference across the two tests to obtain one measure of the strength of preference for each female. We used the average strength of preference for each female in analyses comparing preference across treatments (frequency of male types) and environments (laboratory versus field). No two females evaluated the same two pairs of males across all experiments.

Within each treatment/frequency, we determined whether there was a relationship between strength of preference and female size using a linear regression analysis. To determine whether the different frequencies of male types from our laboratory study influenced strength of female preference, we used a mixed effects model to examine the effects of female size and male frequency on average strength of preference. Since there were three replicates in each treatment, we included tank as a random effect in the model, thus nesting females within tank. To determine how the results from our laboratory treatments compared to the preferences of wild-caught females that had experienced similar frequencies of courter to sneaker males, we used a linear model in which we examined the effects of female size, the frequency of courter to sneaker males and mating experience context (laboratory versus field) on the strength of preference for courter males.

RESULTS

There was no significant difference in the total time that females spent with courter and sneaker males among treatment groups (mean ± SE time spent with both males: virgin females = 2194.0 ± 25.8 s; 1C:5S treatment = 2195.2 ± 31.3 s; 3C:3S treatment = 2244.6 ± 24.6 s; 5C:1S treatment = 2224.7 ± 19.3 s; 3C:19S treatment = 2166.2 ± 22.2 s; 18C:14S treatment = 2228.5 ± 16.4 s; ANOVA: $F_{5,105} = 1.684$, $P = 0.144$).

Virgin Females (Experiment 1)

Virgin females spent significantly more time with courter males than with sneaker males (mean association time ± SE: courter male = 1584.8 ± 69.1 s; sneaker male = 609.2 ± 61.1 s; paired t test: $t_{17} = 7.630$, $P < 0.001$). There was no correlation between female size and the strength of preference for courter males (linear regression: $r^2 = 0.011$, $N = 18$, $F_{1,17} = 0.176$, slope = 12.48, $P = 0.680$; Fig. 1).

Experienced Females (Experiment 2)

Laboratory mesocosms

Females from all three treatments spent significantly more time with the courter male than they did with the sneaker male (mean association time ± SE: 1C:5S treatment: courter male = 1358.8 ± 81.0 s; sneaker male = 836.4 ± 81.3 s; paired t test: $t_{17} = 3.280$, $P = 0.004$; 3C:3S treatment: courter male = 1596.5 ± 79.9 s; sneaker male = 648.1 ± 78.1s; paired t test: $t_{17} = 6.078$, $P < 0.001$; 5C:1S treatment: courter male = 1559.9 ± 88.7s; sneaker male = 664.78 ± 80.1s; paired t test: $t_{17} = 5.331$, $P < 0.001$). There was a significant effect of male frequency on the strength of preference (Table 1, Fig. 2). Females that experienced a sneaker bias had the weakest preference for courter males (mean ± SE = 522.3 ± 159.2 s). In addition, there was a trend for effects of female size and an interaction between female size and male frequency (Table 1, Fig. 2), suggesting that differences in male frequency may influence the relationship between average strength of preference and female size.

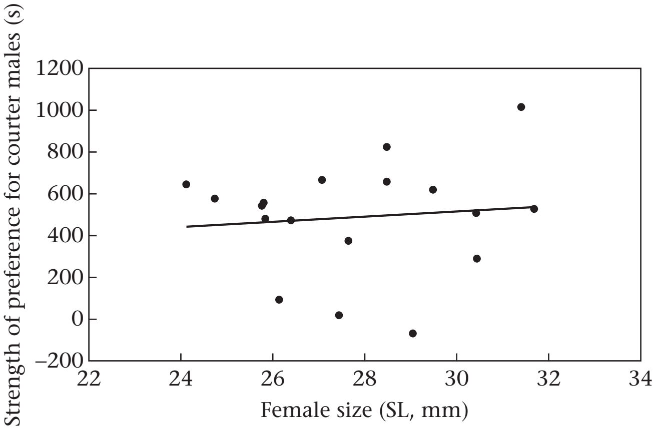

Figure 1. Relationship between female size and strength of preference (difference in time spent with courters and sneakers) for virgin female swordtails, *X. multilineatus*. Negative scores indicate more time with sneaker males; positive scores indicate more time with courter males.

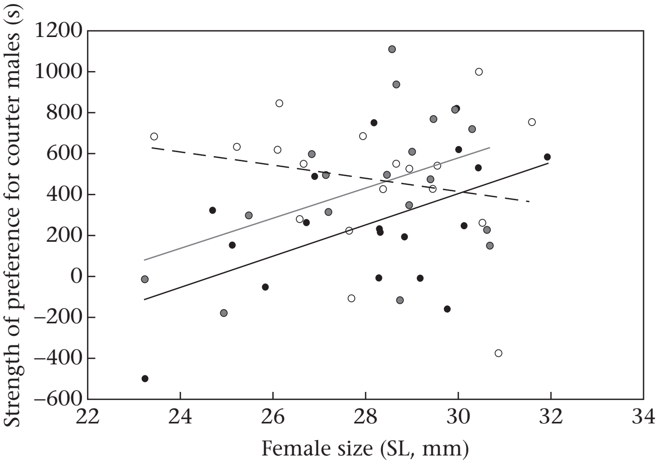

Figure 2. Relationship between female size and strength of preference for courter males in the swordtail *X. multilineatus* for females exposed to sneaker-biased (black circles, black line), equal (white circles, dashed line) and courter-biased (grey circles, grey line) treatments. Negative scores indicate more time with sneaker males; positive scores indicate more time with courter males.

The only treatment in which we detected a significant relationship between female size and average strength of preference was the sneaker-biased treatment (linear regressions: 1C:5S treatment: $r^2 = 0.267$, $N = 18$, $F_{1,17} = 5.814$, slope = 76.543, $P = 0.028$; 5C:1S treatment: $r^2 = 0.177$, $N = 18$, $F_{1,17} = 3.439$, slope = 73.373, $P = 0.082$; 3C:3S treatment: $r^2 = 0.043$, $N = 18$, $F_{1,17} = 0.721$, slope = −31.958, $P = 0.408$; Fig. 2).

Wild-caught

Females collected in March 2009, when the frequency of courter to sneaker males was approximately equal, spent significantly more time with the courter male (mean association time ± SE: courter male = 1547.1 ± 68.8 s; sneaker male = 681.4 ± 67.2 s; paired *t* test: $t_{22} = 6.416$, $P < 0.001$). However, there was no relationship between female size and average strength of preference (linear regression: $r^2 = 0.001$, $N = 23$, $F_{1,22} = 0.012$, slope = 2.561 $P = 0.914$; Fig. 3).

When we compared variation in the strength of preference from the two field samples (2007 sample: Morris et al. 2010; 2009 sample: this study) to the two laboratory treatments with similar ratios of courters to sneakers, we detected a significant interaction between female size and the frequency of males that females experienced (Table 2). There was no significant effect due to where the experience was gained (context: laboratory versus field; Table 2, Fig. 3). For females that experienced sneaker-biased populations, we detected a positive relationship between strength of preference and female size, while there was no relationship with size for those females that had experienced a more equal frequency of courters to sneaker males (Fig. 3).

DISCUSSION

Experience with different frequencies of courter and sneaker males had a significant effect on the strength of preference for courter males in *X. multilineatus*. However, the variation in preference we detected would only produce negative frequency-dependent selection on one end of the distribution and would depend on the frequency of small females (small females had a weaker preference for courters when courters were common). Therefore, variation in

Table 1
Influence of female size and frequency of males in laboratory mesocosms on strength of preference for courter males in the swordtail *X. multilineatus*

Source	*ndf*	*ddf*	*F*	*P*
Female size	1	43.523	3.851	0.059
Male frequency	2	44.228	3.287	**0.047**
Male frequency*female size	2	43.499	3.030	0.059

'Male frequency' indicates the frequency of courter males to sneaker males.

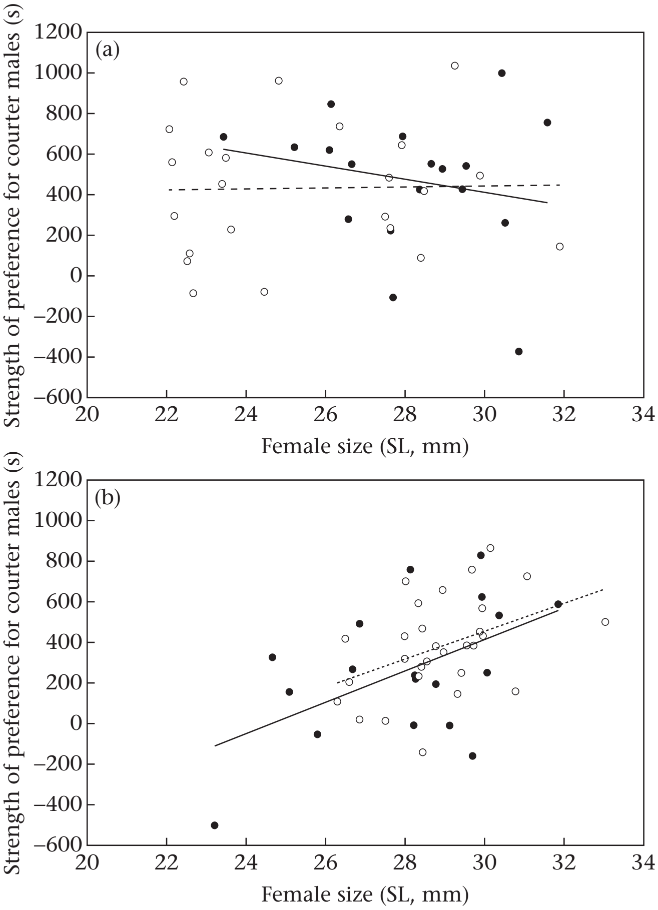

Figure 3. Relationship between female size and strength of preference in the swordtail *X. multilineatus* when the frequency of courter to sneaker males was (a) equal and (b) sneaker biased across laboratory mesocosms (solid circles, solid lines) and field samples (open circles, dashed lines). Negative scores indicate more time with sneaker males; positive scores indicate more time with courter males.

Table 2
Linear model examining the influence of female size, the frequency of male types experienced (sneaker biased or equal) and the environment in which females experienced males (in laboratory mesocosms or in the field) on females' strength of preference for courter males in the swordtail *X. multilineatus*

Source	*df*	*F*	*P*
Female size	1	4.760	**0.032**
Male frequency	1	8.689	**0.004**
Female environment	1	0.384	0.537
Male frequency*female size	1	7.649	**0.007**
Male frequency*female environment*female size	2	0.486	0.617
Error	81		

Overall model fit: $R^2 = 0.160$.

female preference cannot be the only mechanism maintaining the two alternative mating strategies in this species. If variation in preference were the primary mechanism producing negative frequency-dependent selection, we would have expected not only a weaker preference for courter males when they were more common, but also a stronger preference for courters when they were rare. We also found that experience with the different frequencies of males altered the relationship between the strength of female preference for courter males and female size, which could provide further insight into why this preference is plastic. The correlation between female size and strength of preference for courter males was not detected in the inexperienced virgin females, or when the frequencies of males were equal. However, when male frequencies were biased in either direction (courter biased or sneaker biased), the relationship between female size and strength of preference was positive (Figs 1, 2). Below we examine hypotheses for why experience with biased frequencies of males (e.g. courter biased and sneaker biased) would reduce the smaller females' preference for courter males, as well as how this variation in preference could interact with variation in the size distribution of females to play a role in maintaining the genetic polymorphism in this species.

Because female size and fecundity are positively correlated in iteroparous species like *X. multilineatus*, smaller females may be more risk averse. Risk aversion would be adaptive if it helps females reach larger sizes, and thereby attain their maximum reproductive output (Warner 1998). Studies have shown that females alter their preferences to reduce exposure to aggressive male behaviours in Japanese quail (Ophir & Galef 2003, 2004), and the response to male aggression is correlated with female age in satin bowerbirds, *Ptilonorhynchus violaceus*, where younger females are more risk averse (Coleman et al. 2004). For small *X. multilineatus* females, the cost of expressing a mating preference may be too great when exposed to certain frequencies of male strategies, if male aggression is more common at these frequencies. Smaller females reduced their preference in both the courter- and sneaker-biased treatments, but not when the frequencies of the two types of males were equal. Larger females, on the other hand, maintained a strong preference for courter males in all frequencies, which may suggest that large females are better able to handle male aggression, thereby reducing the costs of expressing a mate preference.

The level of male–male aggression may have been greater at both biased frequencies, when males were more likely to be competing with males of the same size. Male–male aggression in swordtail fish becomes more intense in staged contests as the size difference between males decreases (Morris et al. 1995). In addition, in cichlid fish, the composition of male phenotypes in a group can alter male aggression levels such that groups containing one phenotype show higher levels of aggression than those containing a mixture of phenotypes (Dijkstra et al. 2009). The reduction of aggression in mixed groups has been attributed to males biasing aggression towards males of their own phenotype (Dijkstra et al. 2009). This scenario seems particularly likely in species like *X. multilineatus*, where there is such a large size difference between males that use the different alternative mating strategies. Females may incur direct fitness costs when exposed to social contexts with increased male–male competition. For example, female guppies, *Poecilia reticulata*, that experience male harassment produce fewer offspring than females that do not experience male harassment (Ojanguren & Magurran 2007). There may be other changes in the social dynamics across the male type frequencies that influence female mate preference as well. Further studies would help to elucidate whether male aggressive behaviours, or perhaps male courtship behaviours, change with the frequency of courter to sneaker males, and whether these changes in male behaviour help to explain smaller females' reduced preference for courter males.

Previously, we suggested that a relationship between female size and strength of preference could influence the mating success of courters when the size distribution of females changes (Rios-Cardenas et al. 2007). However, given a stable size distribution of females, the pattern we detected in the current study suggests the following: (1) the frequency of the two types of males is involved in producing the relationship between female size and strength of preference, and (2) the reduced preference in smaller females would reduce courter male mating success both when courter males are common (negative-frequency dependent effect) and when they are rare. Therefore, the weaker female mate preference for courters by smaller wild-caught females detected previously and in the present study suggests that this population fluctuates extensively between being courter biased and being sneaker biased. Indeed, female preference could even add to this fluctuation, at least from equal frequency to courter biased and back. Other factors that need to be considered in a model of this system would include natural selection factors that influence the frequencies of the two types of males. For example, as sneaker males also reach sexual maturity sooner, this advantage in combination with a mating advantage with small females, which will be more common in growing populations, could suggest that sneaker males are maintained due to temporal variation in population growth. How variation in female mate preference affects fitness of male morphs is a complex problem, as there are many dynamic factors (e.g. female size distribution and male morph frequencies) that need to be considered. Theoretical approaches such as dynamic state variable models (i.e. optimality models) could be used to provide insight into this problem.

To improve our understanding of the evolution of sexually selected traits, we need a better understanding of the factors that influence female mate preference variation and the dynamics of such factors. Both laboratory and field studies are essential to gaining such insight. Laboratory studies can illuminate exactly which factors have the potential to affect female mate preference, while field studies can highlight the biological significance of those factors. Few studies to date have compared female mate preference variation in the field and the laboratory. The concordance of our results from the laboratory and the field suggest that differences in the frequencies of the alternative mating strategies influence strength of preference for courters and that other factors not included in the laboratory study, such as predation, are not as important. The timescale over which female mate preferences vary will also influence the evolution of female preference and male traits. This requires knowledge of the dynamics of the factors influencing female mate preference.

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