

Original Article

Predator exposure leads to a short-term reversal in female mate preferences in the green swordtail, *Xiphophorus helleri*

Natalie Pilakouta and Suzanne H. Alonzo

Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06520, USA

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Ecological factors have been shown to influence mate choice, resulting in the alteration, loss, and even reversal of mate preference. One such factor is the presence of a predator during mate choice, because females that associate with conspicuous males may experience a higher risk of mortality in high-predation environments. Despite accumulating studies demonstrating predator-induced plasticity in female preferences, it is still unclear how these changes affect the strength or direction of selection. Additionally, even though the temporal dynamics of female plasticity (and the cues that induce it) have important implications for the evolutionary dynamics of sexual selection, little is known about this temporal aspect of mate preferences. Here, we addressed this gap using female green swordtails, *Xiphophorus helleri*, which typically prefer males with long swords. We first examined mate preference in the control (no predator) treatment and asked whether the preference changes immediately following predator exposure. In this experiment, females preferred long-sworded males in the control treatment and short-sworded males in the predator treatment. This suggests that natural and sexual selection may act synergistically in high-predation environments, with both favoring this shorter sword length. We then asked whether females still prefer short-sworded males 24 h after exposure to the predator. Our results demonstrate that the reversal in female mate preference does not persist after 24 h, suggesting that the effect of predators on mating behavior may be more complex than previously thought. Predator encounter rate may thus have the potential to influence sexual selection dynamics in natural populations.

Key words: behavioral plasticity, mate choice trial, mate preference, nonconsumptive effects, predator-prey interactions, sexual selection.

INTRODUCTION

Sexual selection by female choice can lead to the evolution of male sexual traits, such as ornaments and courtship displays (Kirkpatrick 1987). Adaptive mate preferences are often assumed to be static and consistent among females, favoring the extreme expression of male display traits driven by strong directional selection (Chaine and Lyon 2008). It is not clear; however, why we should expect lower plasticity or variability in female preferences than in male signals (Qvarnström 2001), given that male traits may confer different fitness benefits to a female in different contexts (Mays and Hill 2004). There is in fact increasing evidence for among-population, within-population, as well as within-individual variation in female mate preferences (Endler and Houde 1995; Brooks and Endler 2001; Kodric-Brown and Nicoletto 2001; Coleman et al. 2004;

Lynch et al. 2005; Bailey and Zuk 2008; Chaine and Lyon 2008). Ecological factors have been shown to influence mate choice, resulting in the alteration, loss, and even reversal of mate preference (Walling et al. 2008; Botero and Rubenstein 2012).

Such variability in mate preferences could have a significant effect on the rate and direction of sexual selection. It has the potential to slow the exaggeration of male display traits and could thus explain the maintenance of genetic variation in these traits, a widely discussed but open question in evolutionary biology (Brooks 2002). It may also play a role in the presence of multiple ornaments and divergence in mating signals among populations, a precursor to speciation. Nevertheless, the evolutionary significance of variable mate preferences remains a subject of debate (Brooks 2002). It is important to better understand how ecological factors influence variation in mate preferences, as this will affect our predictions about the evolutionary dynamics arising from this variation (Cotton et al. 2006).

One potentially important factor is the presence of a predator or predator cue during mate choice. Females typically prefer

Address correspondence to N. Pilakouta, who is now at Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, West Mains Road, Edinburgh EH9 3JT, UK. E-mail: npila1@gmail.com.

males with conspicuous ornaments or intense courtship displays, which may confer a sexy sons benefit to the female, as well as a good genes benefit if these traits are honest signals of male quality that her offspring may inherit. However, conspicuous males are also more likely to be attacked and experience a higher risk of mortality (Godin and McDonough 2003; Hernandez-Jimenez and Rios-Cardenas 2012); females that associate with these males may thus incur a higher risk of predation (Pocklington and Dill 1995). Moreover, if a female mates with a conspicuous male, her male offspring will also be conspicuous and may experience higher mortality rates (assuming that the male trait is heritable).

Predators can change the abundance of prey populations as a result of direct consumption but also have nonconsumptive effects through changes in various prey traits (Abrams 2007; Peckarsky et al. 2008). Previous studies have typically looked at nonconsumptive effects in the context of foraging behavior, habitat use, growth rate, life history traits, and development (Peckarsky et al. 2008). Yet, the contribution of such effects to sexual selection dynamics in prey populations has been largely overlooked. Nonconsumptive effects can be as important as, or more important than, consumptive effects to prey population dynamics (Peckarsky et al. 2008; Schmitz et al. 2008), so addressing this gap would enhance our understanding of these ecological interactions.

Under predation risk, females may either become less choosy or change the direction of their preference. We might expect a decrease in choosiness when predation risk increases mate searching costs. Mate searching can be costly because higher activity levels increase the probability of encounter with a predator (Magnhagen 1991), so females may be more willing to mate with nonpreferred males. However, if the association with a certain male phenotype itself incurs a cost to the female (i.e., increased risk of predation), then we might expect females to change the direction of their preference, avoiding interactions with those males.

Relatively few studies have examined predator-induced plasticity in female mate preferences, and these are mostly in fishes and insects. Lab-reared Atlantic mollies (*Poecilia mexicana*) alter their initial preference for large males in the presence of a predatory cichlid (Bierbach et al. 2011). In the absence of a predator, female guppies (*P. reticulata*) from a high-predation population prefer brightly colored males, but this preference is reduced when a predator is present (Godin and Briggs 1996). Female crickets (*Gryllus integer*) typically prefer long-bout male calls but are more likely to mate with males with short-bout calls, which are less conspicuous, when cover decreases and thus risk of predation increases (Hedrick and Dill 1993). Female sand gobies (*Pomatoschistus minutus*; Forsgren 1992) and male pipefishes (*Syngnathus typhle*; Berglund 1993) seem to be less choosy under predation threat.

However, it is unclear how changes in the strength or direction of preference vary over time. To the best of our knowledge, there are no studies in the published literature that have examined female mate preference at different intervals from the time of exposure to a predator (but see Melie 2013). Here, we wanted to address that question in female green swordtails (*Xiphophorus helleri*), immediately after exposing them to a predator video and 24 h later.

Green swordtails are small poeciliid fish with sexual dimorphism; males have “swords,” which are ventral caudal fin extensions. The opportunity for sexual selection on male *X. helleri* is among the highest reported in fishes (Tatarenkov et al. 2008), and female preference for males with long swords has been well established in this species (e.g., Basolo 1990, 1998; Trainor and Basolo 2000). However, there is a complete reversal in the direction of this

preference as a result of predator exposure. After being presented with a video in which a predator (*Petenia splendida*) stalked, attacked, and captured a long-sworded male *X. helleri*, females showed a strong preference for the swordless male over the long-sworded male (Johnson and Basolo 2003). Although this study demonstrated a change in preference in a short time frame, it did not address how long this qualitative change in preference persists following predator exposure. Yet, the duration of the reversal in preference following predator exposure has profound consequences for the effect of predator abundance and encounter rate on the strength and direction of sexual selection.

Here, we asked whether the reversal in preference is a general phenomenon found in *X. helleri* populations and, more importantly, whether this reversal persists 24 h after predator exposure. In our first experiment, we examined female preferences in the control (empty tank) treatment and asked whether they change their preference after visual exposure to a predator. We expected that females would prefer long-sworded males in the control treatment and short-sworded males in the predator treatment (as in Johnson and Basolo 2003). In our second experiment, we tested the hypothesis that females would prefer long-sworded males 24 h after exposure to the predator video. This hypothesis was based on the fact that it may not be adaptive for a female to continue preferring the otherwise less attractive male after the end of the predation threat.

It has been previously suggested that plasticity in mate preferences could have a significant effect on the rate and direction of sexual selection (Jennions and Petrie 1997; Widemo and Sæther 1999). We argue that a temporal effect on predator-induced plasticity could have important implications for evolutionary dynamics. Selection on male sexual traits could vary depending on predator abundance and distribution, whether female preferences are plastic, and how long any changes in preferences persist from the time of predator encounter; this may result in fluctuating selection, contributing to the maintenance of variation in male traits.

MATERIALS AND METHODS

All procedures were conducted in accordance with the Association for the Study of Animal Behavior Guidelines and were approved by the Animal Care and Use Committee of Yale University (IACUC protocol #2011–10908).

Study system

All of the swordtails used in this study were first-generation descendants of wild-caught *X. helleri* collected from Princess Margaret Creek in Belize (by a private breeder). Several species of piscivorous fishes were observed in and collected from this creek, including the Neotropical cichlid *P. splendida*, which is a common predator for swordtails (Wessel R, personal communication). The mate preferences of females from this population have not been previously tested. At the time of the mate choice trials, females were between 12 and 18 months old. These fish had not been exposed to any predators before the mate choice trials. All females had been previously exposed to males with long swords and males with short swords, and they were sexually experienced (nonvirgins). Although there is a difference in the strength of preference for large males in virgin and nonvirgin females in northern swordtails (*X. nigrensis*; Wong et al. 2011), there is no evidence that mating experience affects mate preferences in *X. helleri*.

They were reared at 22–24 °C and a pH of 7.5–8 on a 12:12 h light:dark photoperiod. They were fed daily between 10 and 11

AM. Their diet consisted of commercial micropellets and frozen bloodworms on alternate days. Females were kept in groups of 3–4 individuals in 45 and 90-L tanks. Males were kept individually in 10-L tanks. All tanks included a sponge filter and artificial plants for cover. Approximately 30–40% of the water was changed weekly.

Experimental design

For the mate choice trials, we used videos of noncourting males actively swimming in a tank, which were recorded using a Nikon D5000 digital SLR camera on a Sunpak tripod. Each pair of males to be used in the same trial was size matched with only a difference in sword length; we defined long-sworded males as those with swords twice as long as short-sworded males. The males in each of these pairs were also selected to be as similar as possible with regard to color, presence, number, and size of melanin spots. We used 3 pairs of males during the trials. For the control treatment, we recorded a video of a tank with some artificial plants and a bubbler but no fish. For the predator treatment, we used a publicly available video of a captive *P. splendida* swimming around in a tank with some plants and rocks.

We used video playback so that multiple females could be repeatedly presented with the same males and the same predator. This method eliminates confounding factors, such as temporal variation in male motivational state, display rate, and appearance (Kodric-brown and Nicoletto 1997). This makes any observed differences among trials and between treatments more robust, because they are more likely to be due to differences in female preferences rather than differences in the behavior of the males or the predator. Video playback has been successfully used in a number of previous mate choice studies in the green swordtail (e.g., Trainor and Basolo 2000; Basolo and Trainor 2002; Johnson and Basolo 2003).

The experimental setup consisted of a 40-L tank with 3 adjacent monitors. The 2 side monitors (Dell 2007WFPb) projected the *X. helleri* male videos, and the rear monitor (Lenovo 9227-AC1) projected the control or predator video. Two vertical lines on the front glass of the tank divided the tank into 3 compartments, a method that is typically used in mate choice experiments (Johnson and Basolo 2003). Water temperature and other parameters, including pH, carbonate hardness (KH), and general hardness (GH), in the experimental tank were matched to those in the holding tanks. Mate choice trials were conducted between 1 and 4 PM and were recorded using a digital camera on a tripod placed about 1 m in front of the experimental setup.

No delay experiment: mate choice immediately after treatment video

For each dichotomous choice test, we placed a single female in the tank and let her acclimate for 20 min. At this time, nothing was displayed on the monitors. Then, the female was presented with a looped 5-min sequence of either the predator video or the control (empty tank) video. We then turned off the predator or control video and presented the female with the videos of a long-sworded male and of a short-sworded male. To ensure that the female had a fair choice between the 2 males, she was given time to investigate both sides of the tank before we started recording behavioral data; the 20-min mate choice trial started after she had inspected the 2 sides and returned to the neutral zone.

During each trial, we recorded the following variables: association time with each male (defined below), time spent directly interacting with each male (e.g., gliding; swimming in a tight circle using

only the pectoral fins with the genital pore exposed; Liley 1966), and the number of times the female crossed into the neutral zone from 1 of the 2 sides. Direct interaction time was a subset of association time. Association time is the amount of time spent on each of the 2 sides and has been shown to be associated with female choice in this and other species (Forsgren 1992; Walling et al. 2010), so it is a reliable proxy for mate preference. Data were recorded for a total of 20 min, but to avoid any potential side bias exhibited by the female, male videos were switched between the 2 side monitors halfway through the trial.

We used a paired design for this experiment, meaning that we observed each of 20 females in both the control and predator treatments, with 6–8 days between treatments. The order of the 2 treatments was determined randomly for each female. Females were presented with the same pair of males in both treatments. This design allowed us to assess the effect of predation risk on mate choice behavior on an individual level.

Delay experiment: mate choice 24 h after treatment video

This experiment was conducted approximately 3 months after the trials described above. We used the same 20 females as in the first experiment, and we followed a similar experimental design, but with 2-day trials for each treatment. On day 1, we let females acclimate for 20 min and then presented them with a 5-min control or predator video. Females were returned to their holding tank after exposure to the video. The dichotomous mate choice test was conducted 23–25 h later (day 2), after moving the female back to the experimental tank and letting her acclimate for 20 min. We then turned on the side monitors that displayed the male videos and started recording female behavior after she had inspected both sides of the tank and had returned to the neutral zone. Data were recorded for the same variables mentioned above. As in the previous experiment, each female was exposed to both the control and the predator video with 6–8 days between treatments.

Statistical analyses

As association time and direct interaction time are both bounded by observation period, we ran generalized linear mixed effect logistic regression models, assuming a binomial distribution of the errors (Zuur et al. 2009). The models included association or direct interaction time with long- and short-sworded males as the dependent variable (predicting the probability of association or direct interaction), the treatment (control or predator) or experiment (no delay or delay) as a fixed effect, and female as a random effect and are fit using maximum likelihood (ML) methods. We ran these analyses in R (R Core Team 2013) using the glmer function in the lme4 package (Bates et al. 2013). These analyses were done to determine 1) whether the strength and/or direction of female preference differed between the control and predator treatments in each of the 2 experiments and 2) whether female preferences were repeatable in the control treatments across the 2 experiments.

For within-treatment analysis, we calculated a measure of association bias, by subtracting the total time each female spent on the side of the tank closer to the short-sworded male from the total time spent on the side of the tank closer to the long-sworded male. Hence, large positive values suggested a strong preference for the long-sworded male, large negative values suggested a strong preference for the short-sworded male, and values close to zero suggested the female was not choosy. These differences were calculated

for the control treatment and the predator treatment. To determine whether there was a significant preference for either of the 2 males within treatments, we ran a 1-sample sign test ($H_0: M = 0$). Similarly, we calculated a direct interaction bias, by subtracting the total amount of time each female spent directly interacting with the short-sworded male from the total time spent directly interacting with the long-sworded male. We then ran 1-sample sign tests for the 2 treatments ($H_0: M = 0$).

To determine whether females changed their level of activity in response to the control or the predator videos, we used a 2-tailed paired *t*-test to compare the number of times each female crossed into the center of the tank between the 2 treatments. A 2-tailed paired *t*-test was also used to compare the amount of time spent in the neutral zone in the 2 treatments. This was done to look for between-treatment differences in the total amount of time females spent associating with the 2 males, as a measure of sexual responsiveness.

RESULTS

No delay experiment: mate choice immediately after treatment video

Females showed a preference for long-sworded males in the control treatment. They spent more time on the side closest to the long-sworded male than on the side closest to the short-sworded male (sign test: $N_+ = 16, N_- = 4, P = 0.012$; Figure 1a) and spent more time directly interacting with the long-sworded male (sign test: $N_+ = 15, N_0 = 4, N_- = 1, P < 0.001$; Figure 2a). However, the direction of female preference changed after being exposed to the predator video. They spent more time on the side closest to the short-sworded male (sign test: $N_+ = 1, N_- = 19, P < 0.001$; Figure 1a) and more time directly interacting with the short-sworded male (sign test: $N_+ = 0, N_0 = 4, N_- = 16, P < 0.001$; Figure 2a). There was no effect of male identity on association time (Anova: $F = 1.24, P = 0.30$) or direct interaction time (Anova: $F = 0.03, P = 0.97$).

The qualitative shift in female preference was also statistically significant when comparing association bias between treatments (generalized linear model [GLM]: ML estimate treatment = -1.7, standard error [SE] = 0.023, $z = -75, P < 0.001$; Figure 1a). We saw the same pattern for direct interaction time (GLM: ML estimate

treatment = -3.0, SE = 0.13, $z = -23, P < 0.001$; Figure 2a). There was a nonsignificant trend suggesting that females spent more time in the neutral zone during the predator trials (paired *t*-test: $t = 1.83, N = 20, P = 0.08$). The number of times females moved from the sides into the center of the tank was the same in the control and predator treatments (paired *t*-test: $t = 0.58, N = 20, P = 0.57$). Overall, females exhibited a reversal in preference, as a response to the predator video, in terms of both association time and direct interaction time.

Delay experiment: mate choice 24 h after treatment video

Females showed a preference for long-sworded males 24 h after being exposed to the control video. They spent more time in proximity to the long-sworded male than to the short-sworded male (sign test: $N_+ = 18, N_- = 2, P < 0.001$; Figure 1b), and there was a nonsignificant trend of greater interaction time with the long-sworded male (sign test: $N_+ = 10, N_0 = 7, N_- = 3, P = 0.09$; Figure 2b). Females also showed a preference for long-sworded males 24 h after being exposed to the predator video. They spent more time on the side closest to the long-sworded male (sign test: $N_+ = 16, N_- = 4, P = 0.01$; Figure 1b) as well as more time directly interacting with the long-sworded male (sign test: $N_+ = 12, N_0 = 7, N_- = 1, P = 0.003$; Figure 2b). There was no effect of male identity on association time (Anova: $F = 2.74, P = 0.08$) or direct interaction time (Anova: $F = 0.31, P = 0.74$).

There was a stronger association bias for the long-sworded male in the control treatment than in the predator treatment (GLM: ML estimate treatment = -0.25, SE = 0.023, $z = -11, P < 0.001$; Figure 1b). There was no difference in direct interaction bias between the 2 treatments (GLM: ML estimate treatment = -0.11, SE = 0.13, $z = -0.85, P = 0.39$; Figure 2b). Females spent the same amount of time in the neutral zone in the 2 treatments, so the total amount of time associating with the 2 males was the same (paired *t*-test: $t = 0.48, N = 20, P = 0.64$). The number of times females moved from the sides into the center of the tank was the same in the control and predator treatments (paired *t*-test: $t = 0.16, N = 20, P = 0.88$). Overall, females exhibited a preference for the long-sworded male in both treatments.

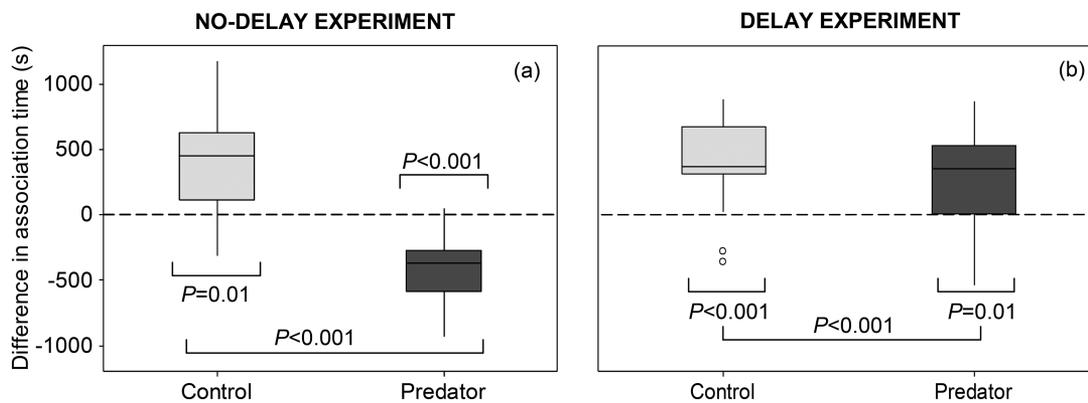


Figure 1

Females change their preference for long-sworded males immediately after predator exposure, spending more time with short-sworded males, but this reversal in preference does not persist 24 h after the exposure. The 2 panels show the difference in association time, as a measure of association bias, for the no delay experiment (a) and delay experiment (b). Positive values suggest a preference for the long-sworded male, and negative values suggest a preference for the short-sworded male. Within treatments, we ran a 1-sample sign test ($H_0: M = 0$) on the differences in association time (no delay experiment: control: $P = 0.01$, predator: $P < 0.001$; delay experiment: control: $P < 0.001$, predator: $P = 0.01$). Between treatments, we ran a generalized linear mixed effect logistic regression model using total association time with the long- versus short-sworded males (no delay experiment: $P < 0.001$; delay experiment: $P < 0.001$).

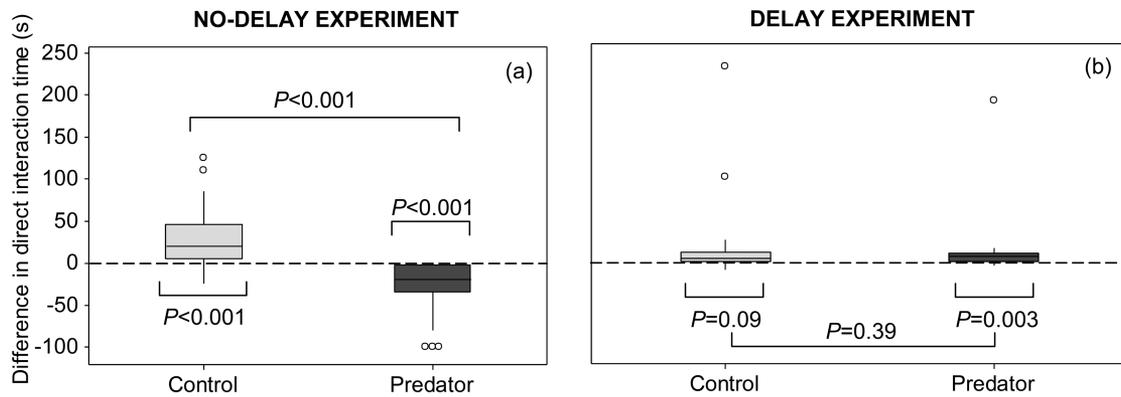


Figure 2

Females change their preference for long-sworded males immediately after predator exposure, interacting more with short-sworded males, but in the delay experiment, they interact more with the long-sworded male in both treatments. The 2 panels show the difference in direct interaction time, as a measure of interaction bias, for the no delay experiment (a) and delay experiment (b). Positive values suggest a preference for the long-sworded male, and negative values suggest a preference for the short-sworded male. Within treatments, we ran a 1-sample sign test ($H_0: M = 0$) on the differences in direct interaction time (no delay experiment: control: $P < 0.001$, predator: $P < 0.001$; delay experiment: control: $P = 0.09$, predator: $P = 0.003$). Between treatments, we ran a generalized linear mixed effect logistic regression model using total direct interaction time with the long- versus short-sworded males (no delay experiment: $P < 0.001$; delay experiment: $P = 0.39$).

Lastly, there was no difference in association time bias (GLM: ML estimate experiment = -0.036 , $SE = 0.023$, $z = -1.6$, $P = 0.12$) across the 2 experiments. However, direct interaction time was lower in the delay experiment than in the no delay experiment (GLM: ML estimate experiment = -0.87 , $SE = 0.13$, $z = 6.6$, $P < 0.001$).

DISCUSSION

Female *X. helleri* showed a clear preference for the long-sworded male in the control (no predator) treatment but reversed their preference right after being exposed to the predator video, favoring the short-sworded male (Figures 1a and 2a). In contrast, our second experiment showed that this reversal did not persist, since females preferred the long-sworded male 24 hours after exposure to the predator (Figures 1b and 2b). This is an example of reversible plasticity, which refers to short-term environmental effects on a behavioral response (Gabriel et al. 2005, Dingemans and Wolf 2013). This is the first study to show reversible plasticity in female mate preferences in response to predation risk, and our results suggest that the effect of predators on mate choice may be more complex than previously thought. If the same population of green swordtails is exposed to different abundances of predators (under otherwise identical circumstances), the outcomes of sexual selection will vary because of differences in predator cues and predator encounter rates. At low predator abundances, there may be directional sexual selection for long swords, whereas at high predator abundances, there may be directional sexual selection for short swords. On the other hand, intermediate predator abundances or variability in predator abundance might result in mate choice patterns that maintain genetic and phenotypic variation in sword length.

In addition to changing the direction of female preference, predators may also affect female movement and sexual responsiveness. We hypothesized that females would be less interested in the males after the predator video, but this was not the case since they spent the same amount of time in the neutral zone in the 2 treatments. There was also no difference in the number of times a female crossed into the center of the tank, which was used as a measure of

female activity. Similarly, in sand gobies, reproduction and female activity did not decrease with increased predation risk (Magnhagen 1993). In contrast, a study on another population of green swordtails found a decline in female interest following exposure to a predator video (Johnson and Basolo 2003).

There were a few notable differences in methodology between our first (no delay) experiment and Johnson and Basolo (2003). First, we used first-generation descendants of a different *X. helleri* population (Princess Margaret Creek, Belize). Second, Johnson and Basolo (2003) gave each female a choice between a sworded and a digitally manipulated, swordless male, which does not reflect the types of males that would be available as potential mates in a natural population, because all sexually mature males have swords. Here, we presented females with males that represented the natural variation in sword length, and we still found a significant reversal in preference even though the sword length difference was less extreme.

In addition, Johnson and Basolo (2003) used a video of a predator stalking, attacking, and capturing a long-sworded male, whereas we used a video of a predator swimming in a tank. The former may have led to an aversive response in the females due to associative learning (e.g., Korpi and Wisenden 2001; Wisenden and Harter 2001; Brown et al. 2011); if females associated the long-sworded male with predation, the change in preference observed in that study may have been an artifact of the methodology used. So, although the main results of our first experiment are consistent with Johnson and Basolo (2003), the reasons underlying the behavior we observed may be different. We believe that our results are more robust because they show that just visual exposure to a predator can change the direction of female preference, even with no prior predator experience and without the confounding factor of aversive associative learning.

For our second experiment, we had a 24-h delay between the treatment video and the mate choice trial. Females spent more time associating with the long-sworded male in both the control and predator treatments, even though there was a greater association bias in the control (Figure 1b). Females spent less time directly interacting with the males in the delay experiment (Figure 2b), perhaps due to a temporal effect, if females became less sexually active

over time. Another possible explanation is that females might have learned that the videos were not responsive males and might have been less motivated to engage in courtship behavior. Rosenthal et al. (1996) found that female interest was higher when *X. helleri* females were presented with actively courting males compared with active but noncourting males. Nevertheless, based on the association time results, there was a clear preference for long swords in both treatments in the delay experiment.

In contrast, a recent unpublished Master's thesis reported that the reversal in mate preference in females from a different *X. helleri* population persisted 24 h after exposure to a predator video (Melie 2013). One possible explanation for this discrepancy is that the duration of the plastic response to predator exposure may vary among *X. helleri* populations. The temporal dynamics of plasticity in mate preferences are largely unexplored, so the causes underlying between-population variation in the duration of mate preference reversal may be an interesting avenue for future research.

The mate preference patterns documented here suggest that it may be adaptive for females to switch back to their initial preference after the end of the predation threat (assuming that female preference for long-sworded males has been favored by selection and that there is no longer a cost of associating with a conspicuous male). Since there is no evidence for direct benefits in this species, this explanation is based on the assumption that females receive indirect benefits from mating with a long-sworded male. Indeed, there is some evidence that sword length may be highly heritable (Campton 1992; Basolo and Wagner 2004; Benson and Basolo 2006), which would confer an indirect benefit through sexy sons to females mating with long-sworded males. Females may also receive a good genes benefit from such matings (Royle et al. 2006).

Regardless of its cause, the evolutionary consequences of this temporary reversal in mate preferences could be significant. Based on the pattern described here, predator abundance and in turn predator encounter rate have the potential to influence the rate and direction of sexual selection on male sword length in natural populations of this species. Thus, there may be differences not just between populations with and without predators but also among populations with different predator abundances and within populations with temporally variable predator abundances.

We know that there is variation in predation pressure among *X. helleri* populations and that males from streams where predators are present have relatively shorter swords (Basolo and Wagner 2004). The common explanation is that longer swords result in higher predation mortality (Benson and Basolo 2006); it has therefore been inferred that natural and sexual selection have an opposing effect on sword length in populations with predators (Basolo and Wagner 2004). However, female preference in response to predator presence is an equally likely explanation for the shorter swords in populations with high predator abundance. Here, we have shown that after visual exposure to a predator, females prefer males with short swords over those with long swords. We thus propose that natural and sexual selection could act synergistically in high-predation environments, with both favoring this shorter sword length. The relative contribution of natural and sexual selection is an open question that future studies could address. It may also be informative to compare sword length not only between high- and low-predation populations but also populations with a temporally variable predation risk.

Studies on the evolution of sexual traits have often ignored the influence of environmental variability and plasticity operating at

different spatial and temporal scales (Cornwallis and Uller 2010). We argue that it would be valuable for future research to consider how the pattern of variability (spatial vs. temporal, coarse grained vs. fine grained) in ecological factors may produce within- and among-individual variation in mate preferences that also vary over the lifetime of a female. Environmental heterogeneity could in turn affect male fitness either directly (e.g., predation) or indirectly (e.g., female mate choice) and ultimately influence the evolution of male sexual traits. In addition, the sensory and cognitive mechanisms underlying female plasticity may also influence the resulting evolutionary dynamics. So far, studies on plasticity in preferences have been mostly descriptive, but it is important for theoretical and empirical studies to directly investigate the evolutionary consequences of this plasticity, as this is still a subject of debate.

Assessing these consequences is not trivial, especially when considering the temporal dynamics of female plasticity that we have documented. In a natural population, changes in mating behavior within and among females may be driven by visual and other predator cues, the presence of which would depend on predator abundance and distribution. These variable preferences could then give rise to qualitatively different patterns of sexual selection on male sword length, in otherwise identical populations: directional selection favoring either longer swords or shorter swords, or maintenance of genetic and phenotypic variation in sword length.

As mentioned earlier, the nonconsumptive effects of predators on prey development, growth, and foraging behavior have been studied extensively, but our results suggest that predator abundance may also influence sexual selection dynamics of prey populations. In addition, our study introduces the possibility of a temporal effect on plasticity in other aspects of prey behavior and prey responses to predator presence. Such reversible plasticity could lead to fluctuating selection and may have important consequences for the maintenance of diversity in general.

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