

RESEARCH PAPER

Predation Risk Reduces a Female Preference for Heterospecific Males in the Green Swordtail

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Abstract

The presence of a predator can result in the alteration, loss or reversal of a mating preference. Under predation risk, females often change their initial preference for conspicuous males, favouring less flashy males to reduce the risk of being detected by predators. Previous studies on predator-induced plasticity in mate preferences have given females a choice between more and less conspicuous conspecific males. However, in species that naturally hybridize, it is also possible that females might choose an inconspicuous heterospecific male over a conspicuous conspecific male under predation risk. Our study addresses this question using the green swordtail (*Xiphophorus helleri*) and the southern platyfish (*Xiphophorus maculatus*), which are sympatric in the wild. We hypothesized that *X. helleri* females would prefer the sworded conspecific males in the absence of a predator but favour the less conspicuous, swordless, heterospecific males in the presence of a predator. Contrary to our expectation, females associated more with the heterospecific male than the conspecific male in the control (no predator) treatment, and they were non-choosy in the predator treatment. This might reflect that females were attracted to the novel male phenotype when there was no risk of predation but became more neophobic after predator exposure. Regardless of the underlying mechanism, our results suggest that predation pressure may affect female preferences for conspecific versus heterospecific males. We also found striking within-population, between-individual variation in behavioural plasticity: females differed in the strength and direction of their preferences, as well as in the extent to which they altered their preferences in response to changes in perceived predation risk. Such variation in female preferences for heterospecific males could potentially lead to temporal and spatial variation in hybridization rates in the wild.

Introduction

Sexual selection through mate choice is an important evolutionary force contributing to morphological and behavioural diversity within and among species (Andersson 1994). Female preference for conspicuous ornaments and intense courtship displays has been well documented in birds (e.g. Andersson 1982), fishes (e.g. Basolo 1990a), reptiles (e.g. Sigmund 1983),

amphibians (e.g. Malacarne & Cortassa 1983) and insects (e.g. Wilkinson & Reillo 1994). This behaviour may be adaptive for females, due to a sexy sons or good genes benefit if these traits are honest signals of heritable male quality (Weatherhead & Robertson 1979). Nevertheless, there is increasing evidence for variation in mate preferences among populations, within populations, as well as within individuals (Endler & Houde 1995; Jennions & Petrie 1997; Brooks &

Endler 2001; Kodric-Brown & Nicoletto 2001; Coleman et al. 2004; Lynch et al. 2005; Bailey & Zuk 2008; Chaine & Lyon 2008; Pilakouta & Alonzo 2014). Thus, a particular male may not be preferred by all females, and an individual female may not always prefer the same type of male. Such variation should not be surprising, given that mate choice is influenced by several factors, including individual experience and condition, inherent perceptual biases and the environmental conditions under which a mating decision is made (Mays & Hill 2004; Hunt et al. 2005; Walling et al. 2008; Amcoff et al. 2013; Ryan & Cummings 2013).

Predator presence, in particular, can play an important role in mate choice, resulting in the alteration, loss or reversal of a mating preference. For example, we might expect females to become less choosy in the presence of predators, because of higher mate searching costs (Crowley et al. 1991). In cases where association with a certain male phenotype itself incurs a potential cost to the female, females may instead change the direction of their preference (Pilakouta & Alonzo 2014). Given that conspicuous males are more likely to be attacked and thus experience a higher mortality risk (Hernandez-Jimenez & Rios-Cardenas 2012; Godin & McDonough 2003), females associating with these males may also incur an increased risk of predation (Pocklington & Dill 1995). Additionally, if the male sexual trait is heritable, male offspring from such matings will also be conspicuous and will potentially suffer higher mortality.

Predator-induced plasticity in mate preferences has received little attention, with a focus to date on fishes and insects. For example, female sand gobies (*Pomatoschistus minutus*; Forsgren 1992) and male pipefishes (*Syngnathus typhle*; Berglund 1993) become less choosy in the presence of a predator. Female crickets (*Gryllus integer*) usually prefer conspicuous male calls but are more likely to mate with males with less conspicuous calls when the risk of predation increases (Hedrick & Dill 1993). In guppies (*Poecilia reticulata*), female bias for males with large body size and bright colouration decreases after predator exposure (Godin & Briggs 1996; Gong & Gibson 1996). These studies demonstrate a plastic female preference for inconspicuous males under predation risk, but they all gave females a choice between different phenotypes of conspecific males. It is still unclear whether females might choose an inconspicuous heterospecific male over a conspicuous conspecific male after exposure to a direct cue of predation risk. Such predator-induced mate preferences for heterospecifics might occur in sympatric species that naturally hybridize. If predator presence indeed influences mate preferences

for heterospecifics, it will affect when and how often hybridization occurs and thus have an effect on species maintenance.

Our study addresses this question using the green swordtail (*Xiphophorus helleri*) and the southern platyfish (*Xiphophorus maculatus*). Heterospecific mating preferences in the *Xiphophorus* genus (Family Poeciliidae) have been studied extensively (e.g. Ryan & Wagner 1987; Hankison & Morris 2002, 2003; Wong & Rosenthal 2006; McLennan & Ryan 2008; Willis et al. 2011, 2012), making this group particularly suitable for our study. This genus comprises two swordtail clades and two platyfish clades (Basolo 1995). In most swordtail species, males have 'swords', which are ventral caudal fin extensions, whereas none of the platyfish species have this secondary sexual trait. Ryan & Wagner (1987) showed that *X. pygmaeus* females prefer larger, sworded heterospecific males (*X. nigrensis*) to smaller conspecific males without swords. Female *X. pygmaeus* also prefer the larger *X. cortezi* males to conspecific males (Hankison & Morris 2002). Lastly, female *X. maculatus* and *X. variatus* prefer heterospecific sworded males to conspecific swordless males (Basolo 1990b; Haines & Gould 1994). These heterospecific mating preferences are consistent with recent studies suggesting that hybridization in the genus *Xiphophorus* is not only possible but probable: hybridization has been very widespread in the evolutionary history of this group, with many of these species being interfertile (Cui et al. 2013; Hyoun Kang et al. 2013). It is worth noting that this earlier work on heterospecific mating preferences focused on females choosing between ornamented heterospecifics and inconspicuous conspecifics, whereas we are investigating female preferences for ornamented conspecifics versus inconspicuous heterospecifics.

For our study, we chose to use *X. helleri* females because (1) female preference for conspicuous males with long swords has been well established in this species (e.g. Basolo 1990a, 1998; Trainor & Basolo 2000); and (2) females reverse the direction of their preference, favouring less conspicuous males with short swords after predator exposure (Johnson & Basolo 2003; Pilakouta & Alonzo 2014). We chose *X. maculatus* as the less conspicuous, swordless heterospecific species, because *X. helleri* and *X. maculatus* occur sympatrically throughout most of their range and can produce viable offspring under laboratory conditions (e.g. Meyer et al. 2006; Schartl et al. 2013). A recent study also reported that there is strong evidence of historical hybridization between *X. helleri* and *X. maculatus* and that it is possible that gene flow between these species is ongoing (Schumer et al. 2013).

We conducted dichotomous choice tests to evaluate the mate preferences of *X. helleri* females for conspicuous *X. helleri* males and the less conspicuous *X. maculatus* males in the presence and absence of a predation threat. Our hypothesis was that females would prefer conspecific males in the control (no predator) treatment but favour heterospecific males in the predator treatment because of the risk of associating with the conspicuous conspecific under predation threat. It is important to better understand how direct cues of predation risk may influence the likelihood of interspecific mating and thus play a role in hybridization rates in natural populations. If a predator encounter causes females to choose an inconspicuous heterospecific male over a conspicuous conspecific male, then predator abundance could influence hybridization rates and gene flow between species.

Methods

Study Animals

All male and female *X. helleri* used in this study were first-generation descendants of wild-caught swordtails collected from Princess Margaret Creek in Belize by a private breeder. *Xiphophorus maculatus* and several species of piscivorous fishes have been observed in this creek, including the Neotropical cichlid *Petenia splendida*. The individuals used in this study came from the same population as those in Pilakouta & Alonzo (2014), where we showed that females prefer long-sworded conspecific males in the absence of a predator but prefer short-sworded conspecific males in the presence of a predator.

Females were between 12 and 18 mo old. All females had previously interacted with conspecific males and were non-virgins, but they were not gravid at the time of the experiment. We chose to use non-virgin females, because they tend to be more responsive when they encounter a male (Basolo 1990a). These females had no previous experience with predators or *X. maculatus* males before this experiment. Male *X. maculatus* were acquired at 12 mo old from Texas State University's *Xiphophorus* Genetic Stock Center. They were reared from the Belize Play II strain, with their ancestors originating from Kate's Lagoon in Belize.

The fish were reared at 22–24°C and a pH of 7.5–8 on a 12:12-h light:dark photoperiod. They were fed once a day between 10 am and 11 am. Their diet consisted of commercial micropellets and frozen bloodworms on alternate days. Females were kept in

groups of three to five individuals in 45-l and 90-l tanks. Males were kept individually in 10-l tanks. All tanks included a sponge filter and artificial plants for cover. We changed 30–40% of the water once a week.

Video Playback Design

For the mate choice trials, we used videos of non-courting males actively swimming in a tank (as in Trainor & Basolo 2000; Pilakouta & Alonzo 2014). We recorded three *X. helleri* and three *X. maculatus* males individually, using a digital camera (Panasonic Lumix DMC-TS10) on a Sunpak tripod. All of the males we used were between 12 and 18 mo old. For each mate choice trial, we randomly selected one of the *X. helleri* and one of the *X. maculatus* videos, such that there were nine possible combinations of conspecific and heterospecific videos. For the control treatment, we recorded a video of a tank containing artificial plants and a bubbler but no fish. For the predator treatment, we used a video of *P. splendida* swimming around in a tank with some plants (as in Pilakouta & Alonzo 2014). *Petenia splendida* is a common predator for swordtails and occurs sympatrically with both species (Basolo & Wagner 2004). All videos were adjusted such that the videos being displayed reflected the fish's true size. While there was no significant variation in male body size within species, there was inevitably a difference between species, as *X. maculatus* males are naturally smaller than *X. helleri*.

Using video playback allowed us to repeatedly present multiple females with the same males. This method eliminates confounding factors, such as temporal variation in male motivational state, display rate and appearance (Kodric-Brown & Nicoletto 1997), making any observed differences among individuals and between treatments more robust. Video playback has been used successfully in previous studies on mating behaviour in this species (e.g. Trainor & Basolo 2000; Basolo & Trainor 2002; Johnson & Basolo 2003; Pilakouta & Alonzo 2014).

The experimental set-up consisted of a 40-l tank (61 × 23 × 33 cm) with three adjacent flat-screen monitors (Fig. 1). The two side monitors (Dell 2007WFPb) projected the *X. helleri* and *X. maculatus* male videos, and the rear monitor (Lenovo 9227-AC1) projected the control or predator video. We marked two vertical lines on the front of the tank to divide it into three equal-sized compartments. The apparatus was illuminated by fluorescent lighting situated approximately 1 m above the experimental set-

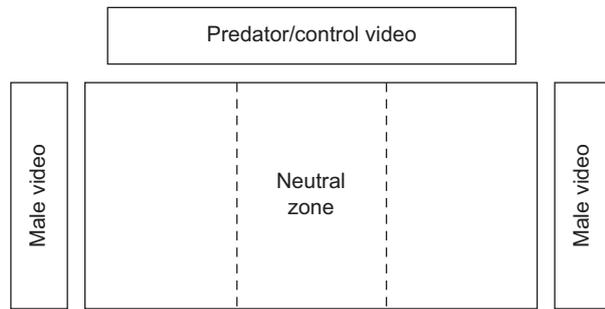


Fig. 1: Experimental setup for dichotomous choice test, consisting of three monitors and a 40-l tank. The rear monitor displayed the control or predator video, which was followed by the conspecific and heterospecific male videos on the two side monitors.

up. We recorded all mate choice trials using a digital camera on a tripod placed approximately 1 m in front of the experimental set-up.

Experimental Protocol

Mate choice trials were conducted between 1 pm and 5 pm. Water temperature and other parameters, including pH, KH (carbonate hardness) and GH (general hardness), in the experimental tank were matched to those in the holding tanks. For each trial, we placed a single female in the tank and let her acclimate for 20 min. Nothing was displayed on the monitors during this period. We then presented the female with a looped 5-min sequence of either the predator video or control video on the rear monitor. After turning off the rear monitor, videos of a conspecific male and a heterospecific male were displayed on the two side monitors. We randomized which of the two male videos (conspecific/heterospecific) was displayed on the left versus the right monitor at the start of each mate choice trial. To ensure that the female had a fair choice between the two males, she was given time to investigate the two sides of the tank before we started recording behavioural data. The 20-min mate choice trial started if the female had inspected both sides and returned to the neutral zone within 2 min (as in Johnson & Basolo 2003). Any females that showed a bias in this initial period ($n = 1$) were excluded from the mate choice trials. To avoid any potential side biases, male videos were also switched between the two side monitors halfway through the trial. We used the same conspecific and heterospecific male videos for the whole duration of a given mate choice trial.

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 one of the two sides. Association time was the amount of time spent on each of the two sides, which is a good indicator of female mate choice in this species (Trainor & Basolo 2000; Walling et al. 2010). Direct interaction time was a subset of association time.

We used a paired design for this experiment, meaning that we observed each of 20 females in both the control and predator treatments, with 7–14 d between the two trials. Females were presented with the same conspecific and heterospecific male videos in both treatments, and the order of the two treatments was determined randomly for each female. This design allowed us to assess the effect of predation risk on mate choice behaviour on an individual level.

Data Analysis

To examine differences in female mate preferences within and between treatments, we used general linear mixed models (LMM). We ran two separate models with association time and direct interaction time as the response variables. Both models included the following fixed effects: treatment (control or predator), the species of the male (conspecific or heterospecific) and the interaction between these two factors. A statistically significant interaction would indicate a change in the strength and/or direction of female preference between treatments. We also assigned female identity, conspecific male identity and heterospecific male identity as random effects. These analyses were run in R version 3.2.0, using the 'lmer' function in the 'lme4' package (Bates et al. 2013). All models were fitted using maximum likelihood methods.

To compare individual-level female preferences within and between treatments, we calculated a measure of association bias, by subtracting the total time each female spent on the side of the tank closer to the heterospecific male from the total time spent on the side of the tank closer to the conspecific male. These differences were calculated separately for each treatment. Large positive values suggested a strong preference for the conspecific male, large negative values suggested a strong preference for the heterospecific male, and values close to zero suggested the female was not choosy.

To determine whether females changed their level of activity in response to predator exposure, we used a two-tailed paired *t*-test to compare the number of times each female crossed into the centre of the tank

between the two treatments. A two-tailed paired *t*-test was also used to compare the amount of time spent in the neutral zone in the two treatments. This was done to look for between-treatment differences in the total amount of time females spent associating with the two males, which can serve as a proxy for sexual responsiveness.

Ethical Note

The protocols used in this experiment were conducted in accordance with the Association for the Study of Animal Behaviour guidelines. All procedures were approved by the Animal Care and Use Committee of Yale University (IACUC protocol #2011-10908).

Results

Treatment (control or predator) and the species of the male (conspecific or heterospecific) did not have an overall effect on female association time (LMM *Treatment*: LR $\chi^2 = 0.36$, $p = 0.55$; *Male species*: LR $\chi^2 = 2.73$, $p = 0.10$). However, there was a statistically significant effect of the interaction between treatment and the species of the male on female association time (LMM: LR $\chi^2 = 7.37$, $p = 0.007$). This interaction reflects that females spent more time associating with the heterospecific male in the control treatment, but they did not show a preference for either male after being exposed to the predator video (Fig. 2). The amount of time a female spent directly interacting with a male did not depend on the species of the male (LMM: LR $\chi^2 = 0.30$, $p = 0.58$), the

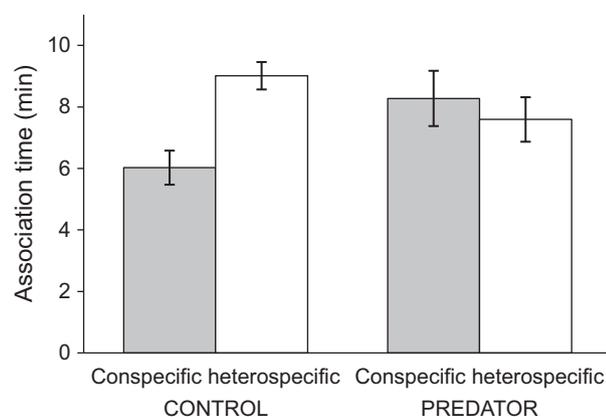


Fig. 2: Amount of time (mean \pm SE) females spent associating with the conspecific (grey) and heterospecific (white) male in the control and predator treatment during a 30-min mate choice trial. Females spent more time associating with heterospecific males in the control treatment, but after predator exposure, they associated with conspecific and heterospecific males equally.

treatment (LMM: LR $\chi^2 = 0.81$, $p = 0.37$), or the interaction between these two factors (LMM: LR $\chi^2 = 0.23$, $p = 0.63$). None of the random effects included in our models were statistically significant.

Female activity was overall unaffected by exposure to the predator video. The total amount of time females spent in the centre of the tank did not differ between treatments (paired *t*-test: $t = 1.2$, $p = 0.24$). Moreover, the number of times females moved from the sides into the centre of the tank was the same in the control and predator treatments (paired *t*-test: $t = 1.3$, $p = 0.20$).

On average, females seemed to spend more time associating with the heterospecific male in the control treatment but showed no strong preference between the heterospecific and conspecific male in the predator treatment (Fig. 2). Nevertheless, when looking at preferences on an individual level, there was substantial variation among females in terms of which male they preferred within each treatment, as well as the magnitude and direction in which their preference changed between treatments (Fig. 3).

Discussion

Xiphophorus helleri females preferred the less conspicuous *X. maculatus* males over the sworded *X. helleri* males in the control treatment. This

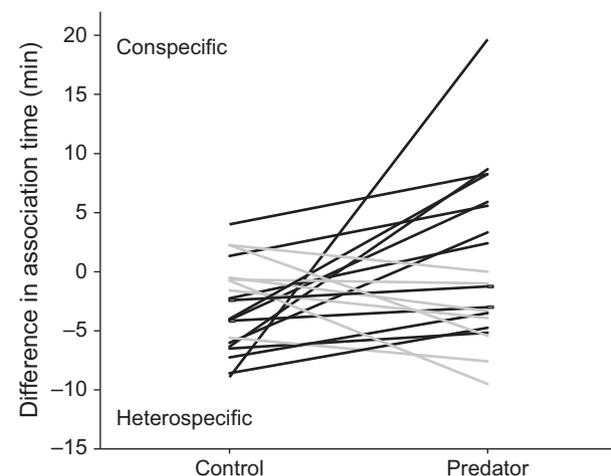


Fig. 3: Behavioural reactions norms for individual females, where the environmental gradient is presence or absence of a predation threat, and the response variable (behavioural trait) is association bias. Positive values suggest a preference for the conspecific male, and negative values suggest a preference for the heterospecific male. The majority of females spent less time on the side closest to the heterospecific in the predator treatment than in the control treatment (black). However, some females associated more with the heterospecific in the predator treatment than in the control treatment (grey).

preference did not persist after predator exposure: on average, females were non-choosy in the predator treatment (Fig. 2). We also documented striking between-individual variation in the degree of behavioural plasticity in response to predator exposure, using females from a single population. Within each of the two treatments, different females preferred different males and also varied in the strength of their preference, with some females being non-choosy. Between treatments, there was variation in both the degree and direction of plasticity in female preferences, as indicated by the slopes of the behavioural reaction norms (Fig. 3). Overall, we find that predation risk causes a switch from preferring heterospecific males in the absence of predators to exhibiting no preference between sworded conspecifics and swordless heterospecifics in the presence of predators. Yet, we also find substantial variation in the strength of heterospecific mate preference among females in the absence of a predator and in the extent of the predator-induced change in preference.

'Foreign-mate preferences', such as the one reported here, are not uncommon and have been observed in various taxa, including the jumping spider *Habronattus pugillis* (Hebets & Maddison 2005) and the Blue Waxbill, *Uraeginthus angolensis* (Collins & Luddem 2002). In fact, preferences for heterospecifics may partly explain the finding that a large proportion of the genomes of most *Xiphophorus* species is derived from hybridization (Cui et al. 2013). However, our results are surprising because females typically prefer conspicuous males and avoid them when there is a high risk of predation (e.g. Johnson & Basolo 2003; Pilakouta & Alonzo 2014). We thus expected that *X. helleri* females would prefer the swordless heterospecific male over the sworded conspecific male in the predator treatment, not in the control treatment.

Instead, we found that female preference for the heterospecific male was reduced after exposure to the predator video. Even though this pattern was unexpected, it is important to note that we used the same methodology and individuals from the same population as in Pilakouta & Alonzo (2014). In that study, females expressed preferences that were consistent with earlier work (Gong & Gibson 1996; Johnson & Basolo 2003): females preferred conspicuous conspecifics in the absence of a predator and less conspicuous conspecifics in the presence of a predator (Pilakouta & Alonzo 2014). Therefore, our findings are unlikely to be due to the experimental setup or the conditions of the study in general.

One potential explanation for the heterospecific preference in the control treatment is that females

were showing a bias for the novel male phenotype. Neophilia, the attraction to novel stimuli, is one of the hypotheses proposed to explain the maintenance of male colour polymorphism and female preference for novel male colour patterns in guppies, *Poecilia reticulata* (Hughes et al. 1999, 2013), which are in the same family (Poeciliidae) as *Xiphophorus*. In addition, Verzijden et al. (2012) showed that although female familiarity with a certain male phenotype can lead to a positive preference bias for that phenotype, it can also induce aversion as in the case of the swordtail *X. malinche*. In zebra finches (*Taeniopygia guttata*), variation in neophilia among females in the context of approach to novel objects reflects variation in reproductive strategies (Schielzeth et al. 2011). Lastly, in some cases, novel phenotypes arising from hybridization may be more attractive to females of the parental species (Rosenthal 2013).

After exposure to the predator video, there was a reduction in the females' preference for the heterospecific male. We suggest that females might have become more neophobic because of the risk of predation. There is evidence that neophobia (i.e. the generalized avoidance response to novel stimuli) is phenotypically plastic and that predation risk plays a role in this plasticity: one way to avoid predation is to be frightened of anything that is new (Brown et al. 2013). In our experiment, some females may have changed their preference due to risk-induced neophobia, thus favouring the conspecific because of familiarity.

Regardless of its underlying cause, the observed predator-induced decline in female preferences for heterospecific males could have important implications for ecological and evolutionary dynamics. Accumulating evidence suggests that environmental disturbances can break down hybridization barriers, potentially leading to introgression into parental lineages, the merging of gene pools or hybrid speciation (Rosenthal 2013). Thus, if the trend we have documented accurately represents a pattern occurring in natural populations, predation pressure may affect the likelihood of interspecific mating and consequently play a role in hybridization rates and the maintenance of species.

Lastly, when looking at mate preferences on an individual level, there was substantial among-female variation in association bias in the two treatments (Fig. 2). Within-population variation in behavioural plasticity among individuals has been a topic of increasing interest in recent years (Jennions & Petrie 1997; Wagner 1998; Wolf et al. 2008; Coppen et al. 2010; Dingemanse et al. 2010; Mathot

et al. 2011, 2012; Westneat et al. 2011; Dingemanse & Wolf 2013; Han & Brooks 2013), but variation in mate preference plasticity has been largely ignored. We are not aware of any other studies reporting individual behavioural reaction norms in the context of mating preferences across environments (e.g., low vs. high risk of predation). Here, we show that individuals from the same population differ in their preference for heterospecifics versus conspecifics in the absence of a predator, as well as in the extent to which they alter their preferences in response to changes in perceived predation risk. Variation in behavioural plasticity can result from additive and interactive effects of past experiences, current individual condition and genetics (Dingemanse & Wolf 2013). In our study, all individuals were exposed to similar environmental conditions in the laboratory, so it is more likely that the variation we observed was due to intrinsic differences among females. If variation in propensity to hybridize is heritable, interspecific matings will involve a non-random set of individuals in the population (Schielzeth et al. 2009), which can have important consequences for the evolutionary trajectory of hybrid lineages (Rosenthal 2013).

Our findings raise interesting questions for future studies to address, as it is still unclear what the proximate and ultimate causes of the among-individual variation in mate preference plasticity are, whether this variation is adaptive, and how selection acts to maintain it. The presence or absence of this variation, as well as whether or not it is heritable, can have significant implications for ecological and evolutionary dynamics (Dingemanse & Wolf 2013). Another suggestion for future research is to investigate whether predation risk reduces the preference for conspicuous heterospecific males in species in which females have been shown to prefer sworded heterospecifics, such as *X. pygmaeus* (Ryan & Wagner 1987), *X. maculatus* (Basolo 1990b) and *X. variatus* (Haines & Gould 1994). If that is indeed the case, the frequency of encounters between females and predators may contribute to variation in the frequency of interspecific mating between populations with different predator abundances.

In summary, it has been well established that predators can have important non-consumptive effects on prey populations by causing changes in prey behaviour (Lima & Dill 1990; Peckarsky et al. 2008; Schmitz et al. 2008), such as mate choice for conspecific males (e.g. Hedrick & Dill 1993; Godin & Briggs 1996; Johnson & Basolo 2003; Pilakouta & Alonzo 2014). Here, we provide novel insights into how predation risk may also influence female

preference for heterospecific males. Our findings suggest that predation pressure may affect the likelihood of interspecific mating, which could have important implications for ecological and evolutionary dynamics. Moreover, the observed variation among females in their mating preference for conspecifics versus heterospecifics and in how they change their preferences in response to predation risk could lead to temporal and spatial differences in hybridization rates in natural populations.

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