

Predator exposure alters female mate choice in the green swordtail

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Female green swordtails, *Xiphophorus helleri*, show a mating preference for males with brightly colored, elongated swords. This preference is thought to be due to a preexisting receiver bias favoring longer sworded males. In this study, we examined variation in the expression of this sword bias in females. Specifically, we tested the hypothesis that an increase in perceived predation risk will decrease female response to males with longer swords. We used a video playback experiment to evaluate female choice between two recordings of a displaying male that differed only in sword length. We scored responses of females to these recordings immediately before and after they had been exposed to a video recording of a predation event between a cichlid and a male possessing a long sword. We found that prior to exposure to this predation event, females preferred the male with the longer sword. However, after exposure to the predator, females altered their mating response, preferring the male with the sword removed. Exposure to the predator also caused an increase in the frequency with which females moved from potential mating positions to a neutral zone. The results presented here suggest that the female preference for males with longer swords can be modulated based on the perceived risk of predation. *Key words*: behavioral modulation, female choice, predation, receiver bias, sexual ornament, sexual selection, swordtails, video playback experiments, *Xiphophorus helleri*. [*Behav Ecol* 14:619–625 (2003)]

Female mating decisions are shaped by a combination of factors, including both intrinsic female preferences and the environmental context in which decisions are made (Endler and Théry, 1996; Houde, 1997). An important environmental factor that may affect female choice is predation risk. Conspicuous male traits that attract females can also attract predators, thereby increasing mortality risk to females that associate with conspicuous males (Hedrick and Dill, 1993; Pocklington and Dill, 1995). Hence, changes in predation environment can have a substantial effect on the expression of female mating behavior (Berglund, 1993; Forsgren, 1992; Wagner, 1998). For example, wax moths reduce their sexual displays of wing fanning in response to increased predation risk by bats (Jones et al., 2002). In theory, such behavioral modulation could apply to any mating preference, even those underpinned by preexisting sensory biases (Basolo, 1990b; Christy, 1995; Endler and McClellan, 1988; Kirkpatrick, 1987; Ryan et al., 1990) or by biases that originate at higher levels of information processing (Basolo, 1990b, 1996).

Mating preferences in female Poeciliid fishes have long interested behavioral ecologists (Houde, 1997; Meffe and Snelson, 1989). Two genera that have received considerable research attention are *Poecilia* and *Xiphophorus*. Experimental results suggest that female guppies, *P. reticulata*, prefer males that are more conspicuously colored (Houde, 1987), that display at higher rates (Brooks, 1996), and that have larger caudal fins (Bischoff et al., 1985) and larger body size (Reynolds, 1993; Reynolds and Gross, 1992). However, both male mating behavior (Endler, 1987; Magurran and Seghers, 1990; Reynolds, 1993) and female preference for more conspicuous males (Gong and Gibson, 1996) decrease in

the presence of predators. Moreover, female preferences for larger males disappear in bright light, a response ascribed to greater predation risk (Reynolds, 1993; Reynolds et al., 1993). Hence, female guppies show plasticity in mating decisions based on the presence or absence of predators. A similar pattern might exist in the green swordtail, *X. helleri*. The sword is a male sexually dimorphic trait characterized by three colored stripes on the caudal fin. In green swordtails, the sword consists of a set of ventral fin rays that extend posteriorly beyond the caudal fin margin. Females are known to prefer larger males (Basolo, 1998b; Rosenthal and Evans, 1998), males with longer swords (Basolo, 1990a), and males with complete expression of the composite sword trait (Basolo and Trainor, 2002). Moreover, the strength of the female preference increases as a function of increasing sword length (Basolo, 1998a; Trainor and Basolo, 2000). Whether female preference for the sword changes under predation threat remains unknown.

A preexisting receiver bias appears to contribute to the female preference for the male sword in green swordtails (Basolo, 1990b). A hallmark of preexisting mating biases is that the preference for a stimulus evolves prior to the trait it favors (Basolo, 1990b; Christy, 1995; Endler and McLellan, 1988; Kirkpatrick, 1987; Ryan, 1990). Such biases can arise at the level of the peripheral sensory system or can arise at a higher cognitive level where information from multiple sources may be assembled to produce a biased response (Basolo and Trainor, 2002; Endler and Basolo, 1998). In green swordtails, the mechanistic cause of the bias favoring the sword is still not known. What is clear is that the strength of female response to a sword has changed over evolutionary time. Phylogenetic evidence indicates that the bias arose before the appearance of the sword (Basolo, 1990b, 1996). However, this bias has changed in strength since the origin of the sword, now being weaker in swordtails than in their unsworded sister group (Basolo, 1998a). One explanation for this result is that preference strength has decreased in swordtails, perhaps due to increased predation risk to swordtail females that associate with more conspicuous males. For example, comparisons within *X. helleri* show that males from populations that lack piscivorous fish predators have

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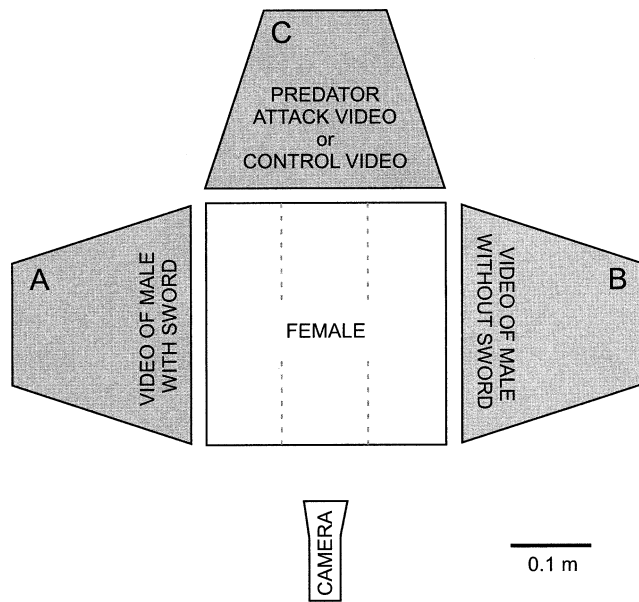


Figure 1

Experimental tank setup used to examine female response to male sword length. Shaded areas represent monitors used to project video images to a focal female housed in the square central tank. Monitors A and B showed images of a displaying male (videos of males were randomly assigned to these monitors at each trial). Monitor C showed images of a fish predator attacking a male with a sword. The dashed lines depict the visual subdivision of the tank into two sides and a central zone. The camera drawn here demonstrates its position relative to the tank, but it was actually positioned farther back. A description of the experimental protocol is given in the text.

relatively longer swords than males from populations that naturally coexist with piscivorous fishes (Basolo and Wagner, in review). Moreover, some predators of pygmy swordtails (*X. nigrensis*) also exhibit a bias for the sword (Rosenthal et al., 2001). Thus, predation environment provides an ecological context in which exhibiting a preference for the sword could be deleterious to females. If this risk is strong enough, we would expect to see an evolutionary decrease in the strength of the preference, as described above, or a facultative change in mate choice based on female assessment of current predation risk.

Behavioral responses across a diverse range of animals have been successfully tested using video presentations (Clark and Uetz, 1990; D'Eath and Dawkins, 1996; Goncalves et al., 2000; Macedonia and Stamps, 1994). Such video techniques have been particularly effective in female mate choice studies in fishes, including guppies (Kodric-Brown and Nicoletto, 1997), sticklebacks (McKinnon, 1995; Rowland et al., 1995), and swordtails (Rosenthal and Evans, 1998; Trainor and Basolo, 2000). However, video presentations of predators to females have not been conducted. By using video to simulate a predation event, individual differences in predator and prey behavior can be controlled. Similarly, using video stimuli of displaying males provides an efficient way to control for the effects of individual differences in male mating behavior on female mating decisions.

In this study, we tested the hypothesis that exposure to a predator will modify how females respond to the male sword. We used a video-playback design to control for differences between male stimuli and to present females with a uniform threat of predation. We found that females preferred males with long swords to males with no swords before a predation event but that this preference declined

after exposure to a predation event. This finding indicates that females can assess environmental conditions and use this information to modify their mating behavior.

METHODS

Study system

Female *X. helleri* tested in this study were third- and fourth-generation descendents of fish collected from Savannah Stream, approximately 40 km west of Belize City, Belize. This stream contains a diverse community of fishes, including the piscivorous cichlid fish, *Petenia splendida*. Females from Savannah Stream tested in the laboratory have previously shown a strong preference for longer swords, as evidenced both by live interactions (Basolo, 1998a) and by females presented with video recordings of courting males (Basolo and Trainor, 2002; Trainor and Basolo, 2000).

We reared females under common environmental conditions of 12:12 h light–dark schedule at 24°C on a diet of live brine shrimp, commercial flakes, and liver paste, the same conditions experienced by laboratory progenitors of the focal fish. The rearing design thus minimized the possibility that differences in behavior among fish were due to environmental effects. Fish were reared in 2.0-l tanks in groups of two or three and were transferred to their own tanks as each approached sexual maturation. Although females had experienced males with swords before testing, females had never been exposed to a predator.

Experimental setup and video playback design

We designed a video stimulus playback system wherein females were allowed to exhibit mating response toward videos of courting male swordtails, both before and after exposure to a simulated predation-risk event (described below). Previous work has shown that video playback of male courting behavior elicits natural responses by *X. helleri* females (Trainor and Basolo, 2000) but has the advantage that male traits can be digitally altered to create different experimental stimuli. To determine whether females would respond differentially to males depending on sword length, two male stimulus tapes were presented to females simultaneously (per Trainor and Basolo, 2000): a video stimulus male with a naturally long sword that extended beyond the caudal fin margin, and a video stimulus male in which the sword had been digitally removed so that it did not extend beyond the caudal fin margin. Each male stimulus was looped to create a video sequence 20 min in length. In addition, we created two 10-min video sequences designed to expose females to one of two levels of perceived predation risk: (1) a high-risk predation treatment that displayed the predator *P. splendida* stalking, attacking, and capturing a long-sworded male *X. helleri* (hereafter referred to as the “predator video”) and (2) a low-risk predation treatment that displayed the same background scene, but lacked images of both the predator and the male swordtail (hereafter referred to as the “control video”). We included a control video treatment in our study to ensure that any change in female mating preference after exposure to the predator was due to predation threat and not simply due to a natural decline in mating interest over the 50-min test period. All video recordings were made under the same environmental conditions in which the female choice experiments were conducted (described below).

To present the videos to females, we used a square glass tank (30.5 × 30.5 × 30.5 cm) with video monitors (Panasonic CT-1384 Y) abutting three sides (Figure 1). Two side monitors were used to project images of the two video stimuli of

courting males, and the rear monitor was used to project the predator or control video. Vertical lines marked on the exposed glass face visually divided the tank into three equal-sized sections (two sides and a center). Water in the tank was maintained at 25°C and filtered for at least 30 min between successive trials. Two VitaLite® bulbs covered in diffusing paper lit the tank from overhead, and a video camera placed 1.5 m from the front glass recorded female behavior. This entire setup was housed in a room with sound-damping walls, and all monitoring was done remotely from an adjacent room.

Experimental protocol

All experimental trials were conducted between 0700 and 1600 h. Each trial included the following steps. First, we introduced a female to the experimental tank and allowed her to acclimate for 30 min. The female was then exposed simultaneously to the two video males (described above); the rear monitor projected an empty tank image. To ensure fair sampling of choice, a female had to investigate both sides within 2 min. After this, we allowed the female to reposition herself in the center area; tapes were then restarted and a 20-min mate choice period began. During this period, we scored the amount of time a female spent (1) directly interacting with the long-sword male; (2) directly interacting with the swordless male; (3) on the side of the tank nearest the long-sword male; and (4) on the side of the tank nearest the swordless male. We also counted the number of times a female switched sides between males and the number of times a female moved from adjacent to a male back into the neutral zone of the tank. After this initial choice period, the side monitors then projected identical images of an empty tank, and the rear monitor projected 10 min of one of the two predation treatment videos described above (predator video, $n = 16$ females; control video, $n = 12$ females). Next, the trial concluded with a 20-min post-treatment mate choice period where females were again allowed to choose between video images of the long-sword or swordless male. Females were thus allowed to demonstrate their response to male sword length, both before and after seeing a long-sword male attacked and eaten by a natural predator or before and after seeing an empty control tank that was devoid of fish.

Analyses

We assayed female response to male videos using three dependent variables: interaction time, side time, and the percentage of side time spent interacting. Because females had the option of not interacting by remaining in the center of the tank, we treated the amount of time a female spent with each male as an independent measure. We tested differences in dependent variables between the two male stimulus videos using ANOVA, with the length of sword (*long* vs. *absent*) treated as a categorical predictor variable. Separate analyses were used to evaluate female response to males before and after exposure to the predation-risk video treatments.

We evaluated the effect of predation risk on mating behavior by comparing female responses to male stimuli before versus after a female was exposed to the 10-min predator (or control) video. Because single females were used throughout each 50-min trial, we used repeated-measures ANOVA (Sokal and Rohlf, 1995). For each set of dependent variables, we ran the analysis two ways, with these sets of analyses run separately for the predator video and the control video treatments. First, to test if predation risk caused an overall change in female mating activity, we pooled data for long-sword and swordless males and then compared the pooled data (for each dependent variable) before versus after

exposure to the predator (or control) video. We also examined female mating response to long-sword males and swordless males separately. This allowed us to determine whether a predation-risk treatment modified female response to males with long swords, males with no swords, or both.

We compared the strength of the female response for the longer sword male relative to the swordless male by calculating a response index (R), defined as:

$$R = (t_1 - t_s)/(t_1 + t_s),$$

where t_1 is interaction time with the long-sword male and t_s is interaction time with the swordless male. This index can range from -1 to 1 , with 0 indicating no difference in response, -1 maximal response for the swordless male, and 1 maximal response for the long-sword male. Finally, we examined the number of times a female switched between males and the number of times a female moved from a side to a neutral position in the center of the tank. For each of these variables, differences before and after exposure to the predator (or control) were tested using repeated-measures ANOVA.

RESULTS

Effect of predator video on female mating response

Before predator exposure, female *X. helleri* showed a clear preference for the male with the long sword. Females spent more time interacting with the long-sword male than with the male in which sword had been digitally removed (least square means: long = 265 s; absent = 109 s; $F_{1,30} = 5.18$; $p = .03$; Figure 2A). There was no difference in the amount of side time females spent between the male with the long sword versus the male with no sword (long = 570 s; shortened = 464 s; $F_{1,30} = 1.0$; $p = .32$; Figure 2B). However, given this equal opportunity to respond to courting males, females spent a greater percentage of side time interacting with the long-sword male (long = 43.1%; absent = 22.8%; $F_{1,28} = 7.42$; $p = .01$; Figure 2C). This resulted in a positive sword response index of 0.38 ± 0.07 in favor of the long sword male (Figure 3).

Exposure to the predator video caused females to change their prior response. After exposure to a predation event, females spent more side time with the swordless male than with the long-sword male (long = 380 s; absent = 575 s; $F_{1,30} = 5.6$; $p = .02$; Figure 2B). Predation eliminated the significant difference in interaction time found before predator exposure, with a trend toward females interacting more with the swordless male (long = 65 s; absent = 130 s; $F_{1,30} = 3.04$; $p = .09$; Figure 2A). There was also a change in the sword response index ($F_{1,15} = 16.1$; $p < .01$) to -0.35 ± 0.06 in favor of the male with no sword (Figure 3). Similarly, predator exposure resulted in a shift to no statistical difference in the percentage of side time females spent interacting with males (long = 15.4%; absent = 22.7%; $F_{1,29} = 1.28$; $p = .27$; Figure 2C).

The predator-induced change in female response was due almost completely to a decline in female interest in the long-sworded male. Planned comparisons of data measuring female response to long-sword males before and after exposure to the predator showed a significant decline for both interaction time ($F_{1,15} = 15.0$; $p < .01$; Figure 2A) and for the percentage of side time spent interacting ($F_{1,15} = 4.3$; $p = .05$; Figure 2C). In contrast, planned comparisons of data measuring female response to swordless males before and after exposure to the predator revealed no statistically significant change in interaction time ($F_{1,15} = 0.31$; $p = .59$;

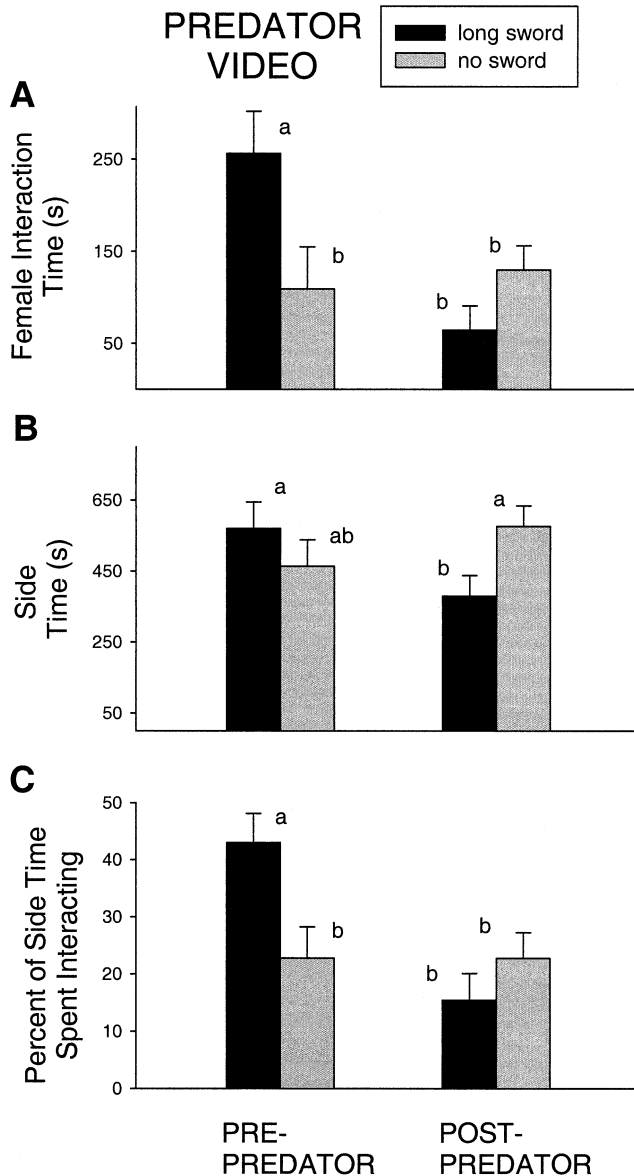


Figure 2

Experimental results of female mating responses to males with long and no swords, before and after visual exposure to the predator *Peteniasplendida*. (A) The mean cumulative amount of time (out of 1200 s) that females interacted with males; (B) the mean cumulative amount of time spent by females in the side area adjacent to the displaying male; (C) the mean percentage of interaction time per opportunity to interact). Error bars depict ± 1 SE. Lowercase letters indicate statistical differences for each response variable based either on simple ANOVA (comparisons between no-sword vs. long-sword males within predation risk treatments) or repeated-measures ANOVA (comparisons before and after predation risk treatment); means with no letters in common are statistically different at $p < .05$.

Figure 2A), side time ($F_{1,15} = 2.07$; $p = .17$; Figure 2B) or in the percentage of time spent interacting ($F_{1,14} < 0.01$; $p = .99$; Figure 2C).

Finally, predator exposure resulted in an increase in the number of times over the 1200-s trial in which females moved from positions adjacent to courting males to a neutral position in the center of the tank (pre-predator = 33.1; post-predator = 44.3; $F_{1,15} = 5.0$; $p = .04$; Figure 4). There was

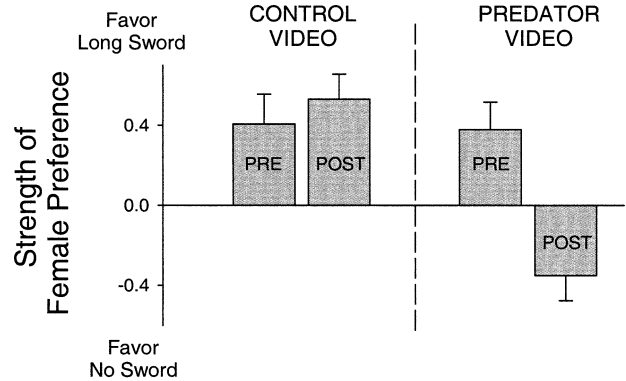


Figure 3

Strength of female response for the long-sword male relative to the shortened-sword male, before and after exposure to the control video and to the predator attack video. Index values have a maximum range of 1 to -1 , with 0 indicating no difference in preference, 1 indicating maximum preference for long-sword male, and -1 indicating maximum preference for short-sword male. Error bars depict ± 1 SE.

no difference in the number of times females switched between the male with the long sword and the male with no sword after predator exposure (pre-predator = 19.8; post-predator = 27.1; $F_{1,15} = 2.2$; $p = .16$).

Effect of control video on female mating response

As in the predator treatment, females in the control trials also showed a preference for the male with the long sword before video treatment exposure. Females spent more time interacting with the long-sword male than with the swordless male (least square means: long = 169 s; absent = 83 s; $F_{1,22} = 5.2$; $p = .03$; Figure 5A). This resulted in a positive sword response index of 0.41 ± 0.15 in favor of the longer sworded male (Figure 3). Females also spent more time on the side of the tank adjacent to the male with the long sword (long = 642 s; absent = 347 s; $F_{1,22} = 12.8$; $p < .01$; Figure 5B). Unlike the predator treatment, there was no difference in percentage of side time that females spent interacting with the long-sword male compared to the male with the digitally removed sword (long = 23.7%; absent = 25.3%; $F_{1,22} = 0.05$; $p = .82$; Figure 5C).

After exposure to the control video, female mating response did not change. Rather, females continued to show a preference for the male with the long sword. Females continued to spend more time interacting with the long-sword male than with the swordless male (long = 178 s; absent = 36 s; $F_{1,22} = 10.7$; $p < .01$; Figure 5A), and, unlike the predator treatment, the sword response index remained positive (0.53 ± 0.16) in favor of the longer sword (Figure 3). Females also continued to spend more time on the side of the tank near the male with the long sword than on the side adjacent to the male with no sword (long = 683 s; shortened = 332 s; $F_{1,22} = 11.4$; $p < .01$; Figure 5B). Moreover, in the control trials, the percentage of side time spent interacting with the swordless male actually decreased relative to the percentage of side time interacting with the long-sword male (long = 24.1%; absent = 12.5%; $F_{1,22} = 5.8$; $p = .03$; Figure 5C), a pattern opposite that observed in the predator treatment (Figure 2C).

Female response to sword length remained constant throughout the control trials. Planned comparisons of female response to the male with the long sword before and after exposure to the control video showed that there were no

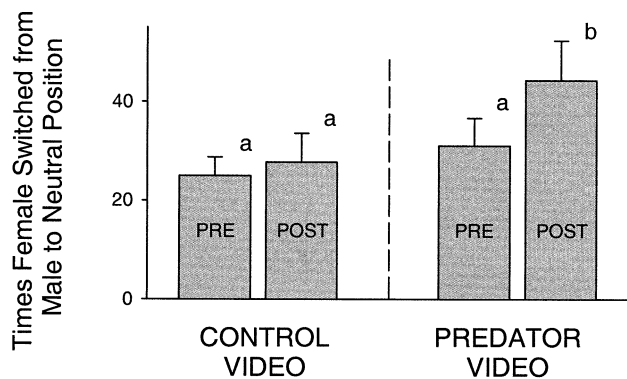


Figure 4

Experimental results comparing female movement before and after exposure to the control video and to the predator video. The figure depicts the number of times in a 1200-s trial that females moved away from a male to the central neutral zone. Lowercase letters indicate statistical differences among treatments for the response variable based on repeated-measures ANOVA (comparisons before and after predator treatment); means with no letters in common are statistically different at $p < .05$.

temporal differences in interaction time ($F_{1,11} = 0.03$; $p = .88$; Figure 5A), in side time ($F_{1,11} = 0.13$; $p = .73$; Figure 5B), or in the percentage of side time spent interacting ($F_{1,11} = 0.05$; $p = .83$; Figure 5C). Planned comparisons of female response to the male with no sword before and after exposure to the control video revealed a decrease in interaction time after exposure to the control video ($F_{1,11} = 5.23$; $p = .04$; Figure 3A). However, there was no significant change in female response to the male with no sword before and after the control video for either side time ($F_{1,11} = 0.02$; $p = .90$; Figure 5B) or percentage of side time spent interacting ($F_{1,11} = 4.15$; $p = .07$; Figure 5C).

In contrast to the response exhibited after exposure to the predator video, exposure to the control video had no effect on the number of times females moved from positions adjacent to courting males to the neutral position in the center of the tank (precontrol = 25.0; postcontrol = 27.8; $F_{1,11} = 0.29$; $p = .60$; Figure 4). The control video also had no effect on the number of times females switched between courting males over the course of the experiment (precontrol = 12.6; postcontrol = 12.3; $F_{1,11} = 0.01$; $p = .91$).

DISCUSSION

Our results demonstrate that in the absence of predators, females show a clear preference for the elongated male sword. On average, females spent more than twice as much time interacting with the male with the long sword than with the swordless male. Females also spent more time in proximity to the male with the long sword relative to the swordless male. Our findings are consistent with previous mate choice studies of green swordtails. Females from this population, as well as from two other populations, showed similarly strong preferences for the sword in both live interactions (Basolo, 1990a) and using controlled video stimuli (Rosenthal and Evans, 1998; Trainor and Basolo, 2000). Thus, the sword preference is repeatable and appears to be common among different populations in this species.

We demonstrate in this study that female green swordtails are capable of flexible mate-choice behavior in response to changes in perceived predation risk. After exposure to the predator video, female interest in the male with the long sword decreased significantly, while female interest in the

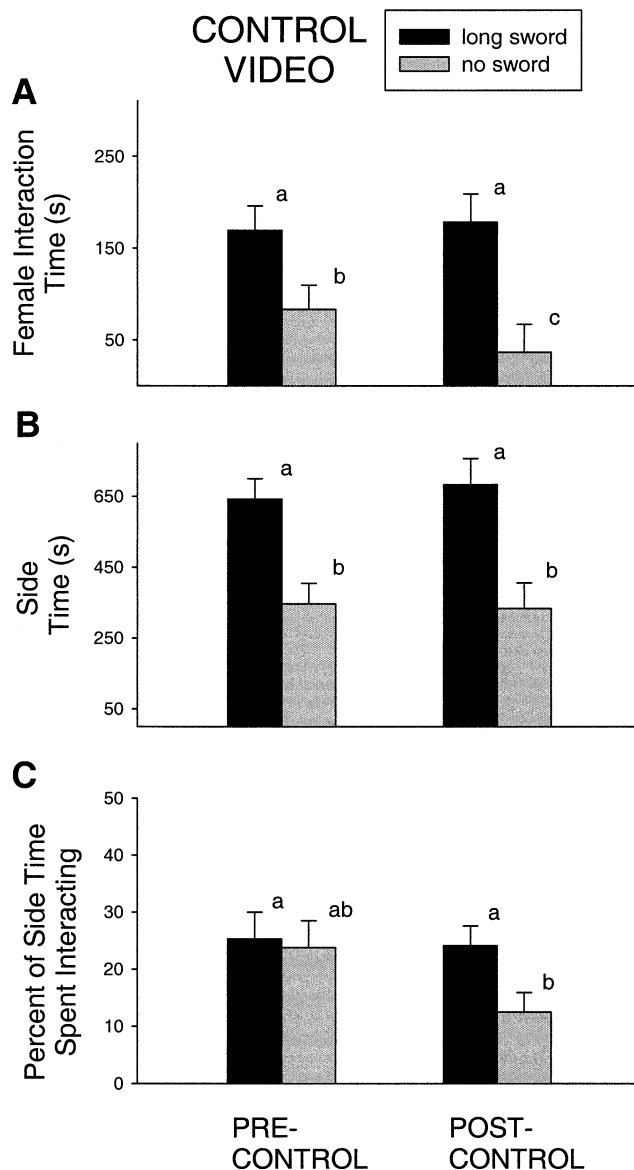


Figure 5

Experimental results of female mating responses to males with long and no swords, before and after visual exposure to an empty tank control video. (A) The mean cumulative amount of time (out of 1200 s) that females interacted with males; (B) the mean cumulative amount of time spent by females in the side area adjacent to the displaying male; (C) the mean percentage of interaction time spent by females adjacent to a male (i.e., a measure of interaction time per opportunity to interact). Error bars depict ± 1 SE. Lowercase letters indicate statistical differences for each response variable based either on simple ANOVA (comparisons between no-sword vs. long-sword males within predation risk treatments) or repeated-measures ANOVA (comparisons before and after predation risk treatment); means with no letters in common are statistically different at $p < .05$.

swordless male actually increased (Figure 2B). The combined total amount of side time spent with both males before versus after exposure to the predator did not change, indicating that females modified their allocation strategy and not their overall willingness to associate with males. The control experiment demonstrates that the observed change in female preference is not simply due to a temporal effect imposed by having the post-predator test follow the pre-predator test. Our data suggest that mating decisions in green swordtails can

change based on perceived predation risk, and for at least one experimental measure (side time) can actually be reversed. Why should females avoid males with long swords when threatened with predators?

A fully developed male sword is a multicomponent trait with a yellow or green stripe layered between two black stripes. Although the sword appears to be favored by females, it might also attract predators. For example, in the closely related pygmy swordtail (*X. nigrensis*), predators exhibit a bias for the male sword (Rosenthal et al., 2001). Thus, females that associate with sworded males may be more likely to encounter predators and could consequently suffer higher mortality. Such might be the case, for example, if the sword physically makes it more difficult for predators to handle males than females or if mature females carrying yolked eggs are easier to capture than adult males. In our study, we intentionally designed the predation stimulus to show a native predator attacking a male green swordtail that had a well-developed sword. However, if predation has selected for plasticity in female behavior, then any encounter with a foraging predator might elicit avoidance of males that are more conspicuous to predators.

Plasticity in female mating behavior can be evaluated as an evolutionary trade-off (as argued in Fuller and Berglund, 1996). Avoiding conspicuous males and spending less time engaged in mating bouts (Figure 4) may reduce predation risk to female green swordtails and thereby extend reproductive life span. However, such avoidance behavior may come at a cost to current reproductive success, particularly if sword length is an indicator of offspring fitness (Williams, 1966), of sperm quality or quantity (Matthews et al., 1997), or of beneficial seminal fluids (Wagner et al., 2001). The adaptation of sperm storage in live-bearing fishes (Constanz, 1989) provides one way by which females could minimize such costs, in that females can mate with preferred males when predators are absent and reduce mating activity when predators are present, without delaying fertilization of mature ova. Observed shifts in interaction time in our data (Figure 2A) support this possibility.

It is apparent that evolutionary changes in preexisting receiver biases can occur (Basolo, 1998a, 2002) and that costs associated with expression of a bias are likely sources of change affecting the strength of female mating responses (Basolo, 1996, 1998a). Mating responses are the result of an integrated process that sums information concerning both internal and external conditions. Some of this information is in the form of stored memories; such appears the case in guppies. Rosenqvist and Houde (1997) found that early life experiences could subsequently affect female mating responses to orange male coloration. Having witnessed a recent predation event directed toward a male with a long sword, it appears that the response of female swordtails to a sword is modulated, with the recent memory overriding the expression of the bias favoring males with longer swords. Why has modulation evolved rather than the elimination of the bias? If the bias currently plays a role in an alternate adaptive context, whether a natural or sexual selection context, it may currently be maintained in that context (Basolo, 2000).

Our findings are consistent with patterns of altered mating behavior in other fishes. An increase in perceived predation risk has been shown to reduce female preference for conspicuous males in both guppies (Dill et al., 1999; Gong and Gibson, 1996) and sand gobies (Forsgren, 1992) and to decrease overall mating activity in pipefishes (Fuller and Berglund, 1996). In the case of green swordtails, there is a preexisting bias in females favoring longer sworded males (Basolo, 1990b). How such biases arise and are maintained remains poorly understood. Our study suggests that the sword

bias need not be expressed under all ecological conditions, perhaps because expression would be costly. Green swordtail females appear to circumvent a potential predation cost by behavioral modulation of the sword bias. In species in which such biases cannot be modulated, the bias may be selected against, providing a potential solution to the puzzle as to why sexually selected traits are commonly lost (Wiens, 2001). It is of interest to note that the strength of the preexisting bias for the sword is weaker in *Xiphophorus*, the genus in which males express swords, than in the proposed sister genus *Priapella*, a group in which males do not express swords (Basolo, 1998a). That the bias in green swordtails is not completely lost but is modulated suggests that under some conditions this bias could be beneficial or that the bias is maintained in an alternative context. Our findings call attention to the question of why receiver biases are maintained even when their expression in a mate choice context could be costly and call for further investigation of the underlying causes of the preference favoring longer swords in swordtails.

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