

Caitlin R. Gabor · Rachel Page

Female preference for large males in sailfin mollies, *Poecilia latipinna*: the importance of predation pressure and reproductive status

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Abstract We examined the effect of predation risk on female association patterns in the live-bearing sailfin molly (*Poecilia latipinna*). We tested two classes of females, with and without the risk of predation by a green sunfish (*Lepomis cyanellus*): (1) postpartum females (maintained with males until visibly gravid, then isolated and tested within 24–48 h of dropping a brood); and (2) non-postpartum females (different females, isolated from males for >50 days). When there was no apparent risk of predation, postpartum females showed a significant preference for large over small males, whereas non-postpartum females showed no size preference at all. When there was an apparent risk of predation, postpartum females maintained their preference for larger males and non-postpartum females continued to show no preference for large or small males. These results suggest that reproductive status (receptivity) plays a greater role in mate preference than predation risk. For postpartum females, the cost of not choosing a preferred mate may outweigh the potential cost of predation. Non-postpartum females either do not benefit from mating or are being indecisive about mating and thus are less likely to be choosy whether or not a predator is present.

Keywords Female mate choice · *Lepomis cyanellus* · Predation · *Poecilia latipinna* · Reproductive status

Introduction

In many species, both mate choice and mate competition favor more conspicuous traits, usually in males (Ryan and Keddy-Hector 1992; Andersson 1994). However, the same conspicuous male traits that are favored by sexual selection may also attract predators, so an evolutionary trade-off may arise (Sih 1994). In addition to the effects of predation on male traits, predation can also have effects on female choice. Models on the evolution of female preferences that include the effects of predation indicate that a female's preference should decrease with greater costs of mate choice (Hubbell and Johnson 1987; Pomiankowski 1987; Real 1990; Crowley et al. 1991; Pomiankowski et al. 1991) and females are expected to be sensitive to predation risk and to become less selective with increasing levels of risk (Real 1990; Forsgren 1992; Godin and Briggs 1996; Gong and Gibson 1996). In addition to being less choosy, females might also prefer to mate with less conspicuous males under increased predation risk. For example, in guppies, *Poecilia reticulata*, females in high-predation populations significantly reduce their preference for more colorful males in the presence of a predator (Breden and Stoner 1987; Godin and Briggs 1996). However, results of studies of female preferences in guppies from low-predation populations are conflicting. Gong and Gibson (1996) found female preference for less conspicuous males in the presence of a predator when using females from low-predation populations whereas Godin and Briggs (1996) did not. One factor not examined in either of these studies that could influence the trade-off between mate choice and predation risk is the reproductive status of females.

It is known that choosiness of females differs depending on their receptivity status. Accordingly, many mate choice researchers select females that are most receptive and are thus most likely to exhibit mate choice (e.g. gravid female fish: *Oryzias latipes*: Howard et al. 1998; *Gasterosteus aculeatus*: Hatfield and Schluter 1996; Nagel and Schluter 1998); female frogs found in amplexus: *Physalaemus pustulosus*: Bosch et al. 2000;

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C. R. Gabor (✉)
Department of Biology,
Texas State University,
San Marcos, TX 78666, USA
e-mail: gabor@txstate.edu
Tel.: +1-512-2453387
Fax: +1-512-2458713

R. Page
Section of Integrative Biology, C0930,
University of Texas,
Austin, TX 78712, USA

Bufo valliceps: Wagner and Sullivan 1995; and female field crickets after their final molt: *Gryllus integer*: Wiegmann 1999).

There are plenty of examples of experiments that examine the effect of predation risk on mate choice (Godin and Briggs 1996; Gong and Gibson 1996) and on reproductive behavior (Endler 1987; review in Magnhagen 1991; review in Sih 1994). However, to our knowledge, no studies have examined the effect of female receptivity status on mate choice under risk of predation. This is especially applicable to live-bearing poeciliid fish, where males have the potential to be sexually active year round but females are usually only receptive for a few days out of a month (Farr and Travis 1986; Snelson et al. 1986; Travis 1989). Brood-cycle stage in poeciliids, as in many organisms, is a critical determinant of a female's receptivity. Poeciliid fertilization is internal and embryos develop within the female until the female gives birth to live fry. A new batch of ova reach maturity near this time, and the female is most receptive to fertilization within a few days of dropping a brood (Liley 1966; Farr and Travis 1986; Snelson et al. 1986; Sumner et al. 1994). The female is usually unreceptive to fertilization for the subsequent interbrood interval (Farr and Travis 1986; Snelson et al. 1986; Sumner et al. 1994), at which point the female drops another brood and the cycle begins again.

Many studies have found female preference for larger over smaller males in poeciliid fishes (Bischoff et al. 1985; Hughes 1985; Ryan and Wagner 1987; Basolo 1990a, 1990b; Ryan et al. 1990; McPeck 1992; Reynolds 1993; Marler and Ryan 1997; Ptacek and Travis 1997; Witte and Ryan 1998; Gabor 1999; Bisazza et al. 2001; Aspbury and Basolo 2002). However, depending on the stage of the brood cycle, some researchers have found no female preference for larger males (Bisazza and Marin 1991; Ptacek and Travis 1997). For example, Ptacek and Travis (1997) found that postpartum and virgin *P. latipinna* females significantly preferred large over small males, but that non-postpartum (not immediately receptive and non-gravid) females did not show any size preference.

The goal of this study was to assess the effect of a predator (green sunfish, *Lepomis cyanellus*) on postpartum and non-postpartum female sailfin molly, *P. latipinna*, preference to associate with large and small males. Females were tested in two states of receptivity: (1) postpartum—females that dropped broods within 24–48 h. Several studies have demonstrated that sailfin mollies are receptive for a 2- to 3-day period immediately after producing a brood, after which they are unreceptive to fertilization until they drop their next brood (Farr and Travis 1986; Snelson et al. 1986; Sumner et al. 1994); and (2) non-postpartum—females that have been separated from males for at least 50 days and have not produced a brood during or after this interval. Prior research on size preferences in sailfin mollies indicates that females in different stages of their brood cycle prefer larger males (Schlupp et al. 1994; Marler and Ryan 1997; Ptacek and

Travis 1997; Witte and Ryan 1998; Gabor 1999). However, Ptacek and Travis (1997) found that non-postpartum females do not show such a preference, whereas Witte and Ryan (1998) and Gabor (1999) found that non-postpartum females did show a preference for larger males. Thus, non-postpartum females may not be consistent in their preferences. We examined preferences of both postpartum and non-postpartum females in the presence and absence of a predator to determine how predation risk and/or receptivity alters female preferences.

Methods

Collection and set-up

Sailfin mollies were wild-caught in Lafayette, Louisiana in September 1997 and April 1998. Three adult green sunfish were caught 15 May 1997 at Brackenridge Field Laboratory, Austin, Texas. The sunfish were maintained in 53-l aquaria. The fish were maintained at 25–30°C in 14L:10D photoperiod conditions using fluorescent lights during the daylight hours. The holding aquaria, plastic isolation tanks, and observation tanks were filled with water (6 ppt salinity) and each contained a water filter, Java moss *Vesicularia dubyana*, and gravel substratum. The mollies were fed TetraMin conditioning food daily, and all fish were fed prior to testing. The green sunfish were fed juvenile sailfin mollies and earthworms (*Lumbricus terrestris*) three times a week.

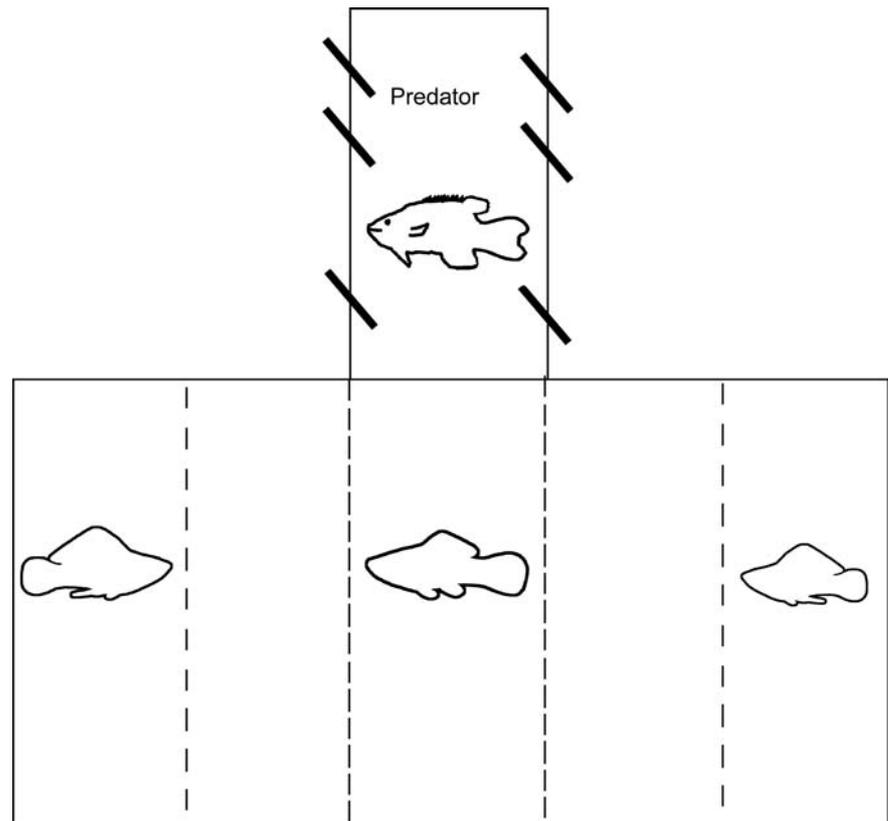
Green sunfish have relatively large mouth gapes for sunfish and are known to prey on fish in the same size range of prey as bass, *Micropterus salmoides* (Werner 1977). Green sunfish have been shown to prey on *Gambusia* spp. (Greenfield and Deckert 1973; Lemly 1985; Smith and Belk 2001), sticklebacks, *G. aculeatus* (Greenfield and Deckert 1973), and plains killifish, *Fundulus zebrius* (Lohr and Fausch 1996). Green sunfish co-occur with sailfin mollies in many parts of their range (Page and Burr 1991) and are known to prey on adults (C.G., personal observation). Additionally, it is known that two species of herons preferentially prey on larger sailfin mollies over small ones (Trexler et al. 1994).

We tested females in one of two stages: (1) postpartum females ($n=10$) were maintained together with different-sized males in 53-l and 37-l communal aquaria, in a female to male ratio of 3:2. When a female became visibly gravid (evidenced by an enlarged abdominal cavity), she was placed alone in a small plastic tank (20.5×13×13 cm). We examined the plastic tanks daily and tested these females within 24 h of dropping a brood. (2) Non-postpartum females ($n=17$) were maintained together in a 53-l aquarium. When testing began, these females had been isolated from males for a minimum of 50 days. We tested non-postpartum females after 50 days to control for female reproductive status because the average brood interval for mollies is 30 days (Travis 1989). None of these females had broods just before or soon after testing, indicating that the females were not receptive and were not likely to have another brood in the near future. Females are unreceptive outside of the 2–3 days after they drop a brood until they drop their next brood (Farr and Travis 1986; Snelson et al. 1986; Sumner et al. 1994). To test all the females during the same time period we did not use the postpartum females to create the non-postpartum females.

Experimental design

In this experiment we examined the effect of an apparent increase in predation risk on the mating preferences of individual female mollies. We tested each class of females under two treatments: (1) predator present, and (2) predator absent. A binary mate-choice apparatus was used to test individual females for their mating

Fig. 1 Top view of the experimental apparatus, consisting of a rectangular aquarium as the female sailfin molly, *Poecilia latipinna*, preference apparatus, perpendicular to a second smaller-sized aquarium housing the green sunfish, *Lepomis cyanellus*. Small-dashed lines indicate the non-preference zone. Large-dashed lines indicate Plexiglas barriers that provide visual, and potentially chemical and mechano-sensory, cues. Diagonal slashes indicate that the sides of the predator aquarium were opaque to prevent the male object sailfin mollies from observing the predator



preferences based on similar designs described by Godin and Briggs (1996) and Gong and Gibson (1996). We conducted the preference tests in a 53-l aquarium (61.0×30.5×30.5 cm) divided into five equal-sized sections (Fig. 1). The two end compartments were separated from the central compartment by transparent Plexiglas dividers with small holes to allow for potential visual, chemical, and mechano-sensory cues during testing. No matings could occur. The central compartment was visually divided into three sections by two lines drawn on the outside of the aquarium. The aquarium contained tan gravel and 18 cm of water. The predator (or nothing) was placed in a 18-l aquarium (30×15×20.5 cm) perpendicular to and abutting the binary choice apparatus (Fig. 1). The central compartment of the choice tank contained a patch of Java moss in the central section to provide shelter for the test female. Three sides of the tank were covered in black plastic to prevent distraction, and the fourth side was covered with one-way film. A 50-W full spectrum incandescent light (General Electric Gro-n-Sho) was suspended 40 cm above the tank, and all other lights were turned off during testing.

For each trial, two males differing in standard length by ≥ 15 mm were selected from a communal aquarium and each was placed randomly in either side of the test tank. The same pair of males was used for both trials to control for variation in male behavior between treatments. The order of treatments was randomized. The test female was chosen from a different communal aquarium from the males and was placed in the center compartment under a rectangular net box (17×12×13 cm). The female was exposed to visual cues from the predator (if present) and to visual and chemical cues from both object males in the end compartments. After a 10-min habituation period, the net box was carefully removed, and for 10 min the female was allowed to swim freely in the center compartment. We recorded the time the female spent within one body length of each male's compartment. All other time was recorded as time spent in the center compartment. The trial was repeated with the males' positions switched to control for side bias. Aquaria water was changed each testing day. Up to

three females were tested each day. We conducted trials from 1200 to 1800 hours, 19 May to 26 June 1998.

Statistical analyses

We analyzed the effect of male size on association preference of postpartum and non-postpartum females both in the presence of a potential predator and without a predator using Wilcoxon signed-ranks test for matched pairs. For statistical analyses, we arbitrarily compared the time each test fish associated with the object fish on the right side of the chamber within trials for both treatments. This method was used to provide statistical independence of data for individual test fish (for rationale see Gabor 1999). If there was a significant preference in a given treatment, then we compared the strength of preference for large males (measured as the amount of time spent with the larger male minus the time spent with the smaller male) between predation treatments using a Wilcoxon signed-ranks test.

We also measured female 'responsiveness' to the treatments as the total time spent with large and small males between both trials over the total time in both trials (1,200 s). Responsiveness scores near 1 indicate one of two things: a high strength of preference for one male (indicated by high responsiveness score and high strength of preference score) or a high degree of movement between two males (indicated by high responsiveness score and low strength of preference score). A responsiveness score near zero indicates little interaction with either male.

Based on Bonferroni's inequality (Snedecor and Cochran 1980), we reduced alpha for postpartum and non-postpartum females. For postpartum females these data were analyzed three times so $\alpha=0.05/3=0.016$; for the non-postpartum females data were analyzed two times so $\alpha=0.05/2=0.025$. We used a two-tailed test for the non-postpartum females because we had no a priori prediction for association behavior. We used a one-tailed test for the postpartum females as previous work has shown that receptive females prefer larger males to smaller ones (Ptacek and Travis 1997).

Results

Non-postpartum females showed no significant preference for large males or small males in both the predation treatments (Table 1). Postpartum females spent significantly more time with large males than small males both when a predator was present and when no predator was present (Table 1).

Because postpartum females showed a preference for large males under both predation treatments, we compared the strength of preference between predation treatments to test if predators decrease the magnitude of the preference for postpartum females. We found that there was no significant difference in strength of preference for large males when postpartum females were tested with and without predators (Fig. 2; Wilcoxon signed-ranks test: $n=10$, $T^+=35$, $z=-0.764$, $P=0.25$).

Postpartum and non-postpartum females showed similar levels of responsiveness to males across both

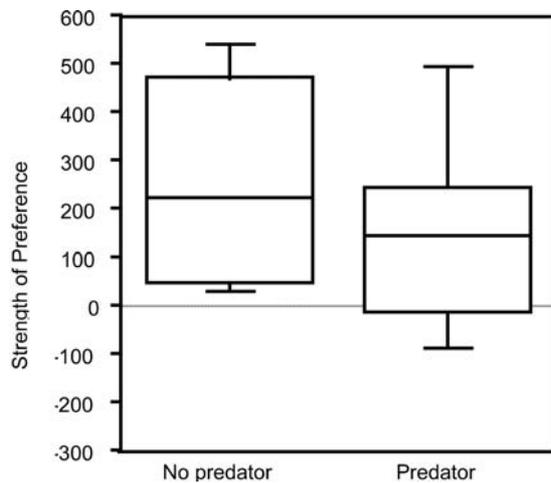


Fig. 2 Strength of preference for large sailfin mollies, *P. latipinna* (time with large male minus time with small male, in seconds), by postpartum female sailfin mollies in the presence and absence of a predator

predation treatments (Table 2). For postpartum females, their high level of responsiveness and their high strength of preference indicates that they prefer large males and do not sample both males very much. On the other hand, the lack of a preference for large or small males by non-postpartum females combined with their high responsiveness indicates that they are interested in males and are sampling both males but are indecisive.

Discussion

We found that female association preference varies between postpartum and non-postpartum females. Postpartum females showed a significantly greater preference for large over small males both without and with a predator present, whereas non-postpartum females showed no preferences in either predation treatment. Previous studies measuring female association preference in mollies show that non-postpartum females (isolated females that had been in contact with males within 18 days of testing) showed a significant preference for larger males (Witte and Ryan 1998; Gabor 1999), whereas Ptacek and Travis (1997) showed that non-postpartum (not isolated and non-gravid) showed no preference for larger males. The results of these studies in combination with our results suggest that when examining female preferences the conclusions reached might be strongly affected by the rearing experiences and the potential receptivity state of the females.

We also found that the strength of preference for large males of postpartum females did not change between predation treatments. Prior research on the effect of predators on mate association has found that predation risk changes female choice in guppies, *P. reticulata* (Godin and Briggs 1996; Gong and Gibson 1996), sand gobies, *Pomatoschistus minutus*, (Forsgren 1992), and crickets, *Gryllus integer* (Hedrick and Dill 1993). Our results contrast with these prior studies. Postpartum females in our study maintained a preference for large males even with the apparent risk of predation. One

Table 1 The mean time \pm SE (in seconds) spent with large and small males by female *Poecilia latipinna* in two reproductive stages tested in two treatments, and values from the Wilcoxon signed-ranks test

| Receptivity and treatment | Mean time \pm SE (s) | | Number | z | T ⁺ | P |
|------------------------------|------------------------|--------------------|--------|--------|----------------|--------|
| | With large male | With small male | | | | |
| Postpartum with predator | 334.90 \pm 58.50 | 167.20 \pm 40.99 | 10 | -2.191 | 49 | 0.014 |
| Non-postpartum with predator | 273.53 \pm 46.16 | 268.88 \pm 44.54 | 17 | -0.497 | 87 | 0.619 |
| Postpartum no predator | 383.80 \pm 53.63 | 129.20 \pm 56.80 | 10 | -2.803 | 55 | 0.001 |
| Non-postpartum no predator | 288.65 \pm 36.74 | 253.82 \pm 48.14 | 17 | -0.355 | 84 | 0.7226 |

Table 2 The mean responsiveness \pm SE of female *P. latipinna* in two reproductive stages toward large and small males when they were tested in two treatments

| Receptivity | Mean responsiveness \pm SE | | Number |
|----------------|------------------------------|------------------|--------|
| | With predator | Without predator | |
| Postpartum | 0.78 \pm 0.069 | 0.71 \pm 0.081 | 10 |
| Non-postpartum | 0.79 \pm 0.033 | 0.79 \pm 0.043 | 17 |

explanation for these differences is that the previous studies using poeciliid fish have used virgin females when examining the effect of predation risk on female choice. These studies show that female choice changes in the presence of a predator (Godin and Briggs 1996; Gong and Gibson 1996). However, the cost of dying due to predation might be higher for virgin females than females that have had a brood at least once, as in our study. Magnhagen (1991) suggested that older individuals would be more choosy when exposed to a predator as compared with younger individuals. Magnhagen (1990) found this to be true for black goby, *Gobius niger*. This may explain the lack of a change in preference of postpartum females in our study due to the presence of a predator. These receptive females are clearly older than virgin females, already have some fitness from at least one brood and thus may be more choosy than virgin females in the presence of a predator.

Finally, we found that in the presence of a predator, non-postpartum females did not show a preference for either male. Because the costs of associating with large males in the presence of a predator might be higher than the benefit of choosing large males for non-postpartum females we expected them to show either no preference or a preference for smaller, less conspicuous males. The latter expectation was not supported, suggesting that non-postpartum females do not select less conspicuous males. Although the former expectation was met, this result is difficult to interpret, as the non-postpartum females also showed no preferences in the absence of predation risk.

An alternative explanation for the behavior of non-postpartum females in the predation treatment is that these females are simply not responsive to males. One way to examine female responsiveness is to examine the percentage of time females spent interacting with males (responsiveness). We found that non-postpartum females showed high responsiveness scores, combined with no preference for large or small males. This indicates that there was a high degree of movement between the two males in both treatments. These results suggest that either non-postpartum females are so interested in mating that any partner would do, or that non-postpartum females are indecisive.

Alternatively, the non-significant results for the non-postpartum females and the lack of difference in strength of preference for the postpartum females between predation treatments may not indicate the lack of importance of perceived predation risk on female preference. We do not think this is a likely explanation for our results, as our design was very similar to those used by Godin and Briggs (1996) and Gong and Gibson (1996) where they did find a significant effect of the presence of a predator on female preference. In addition, Gong and Gibson (1996) were able to elicit these responses even when using an exotic piscivorous predator.

In conclusion, our results suggest that predation risk has little effect on the preference of female sailfin mollies, suggesting that the strength of selection acting via predation on female mate choice in natural popula-

tions may not be as strong as predicted by studies that have only tested virgin females. Furthermore, these results indicate that testing postpartum females instead of, or in addition to, virgin females may give more indication about the costs of mate choice in the wild where not all females are virgin. Testing association preferences of non-postpartum females is contra-indicated.

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