

# SEXUAL HARASSMENT AS A COST FOR MOLLY FEMALES: BIGGER MALES COST LESS

by

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## Summary

Females of many species receive male attention that reflects a conflict between the sexes over reproduction. Here we demonstrate that female sailfin mollies (*Poecilia latipinna*) suffer such a cost via a reduction of their feeding time in the presence of males. Female sailfin mollies spend significantly more time feeding when accompanied by an Amazon molly (*P. formosa*) or a sailfin molly female than when accompanied by a male sailfin molly. Furthermore, we show that male sexual harassment is size dependent and that small males impose a greater cost on females.

*Keywords:* sexual harassment, *Poecilia*, gynogenesis, unisexual, *Poecilia latipinna*, *Poecilia formosa*, guppy.

## Introduction

In many mating systems males use coercion to inseminate females. Male coercion can be costly for females, due to: death of the female (*e.g.* Reale *et al.*, 1996 in feral sheep; common toads IS pers. obs.), increased predation

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risk (e.g. Rowe, 1994), and energy costs (e.g. Watson *et al.*, 1998). Male coercion may also lead to forced shifts in female time allocation (e.g. Magurran & Seghers, 1994; Stone, 1995), mating pattern (Trail, 1985), and strategies that aim at avoiding male coercion (e.g. Palombit *et al.*, 1997; for review see Clutton-Brock & Parker, 1995).

One of the resulting conflicts between the sexes is over the amount of sexual attention a female receives. It seems apparent for males that the more time they spend with females the more opportunities for reproduction they may have. For females, however, surplus attention may be costly, although a certain amount of male attention is necessary for females to facilitate mate choice or to prime females for reproduction. In many lagomorphs, for example, ovulation is induced by copulation (for a review see Nelson, 1995). Costs of surplus male attention may come in various currencies, such as attraction of predators or parasites, reduced vigilance, or reduced feeding efficiency.

In poeciliid fishes the general breeding ecology predicts intensive male sexual harassment. Females have a distinct sexual cycle of roughly 25 days (Parzefall, 1973), and are readily fertilised for only a few days each cycle, just after parturition. In guppies copulations outside those days transfer only relatively small amounts of sperm (Pilastro & Bisazza, 1999), although males attempt to mate with females constantly (Farr, 1980, 1989; Bisazza & Pilastro, 1996). This leads to an extremely male biased operational sex ratio (OSR), and females are likely to receive many more mating attempts than needed for reproduction. As fish with internal fertilisation, female poeciliids have some control over mating access by males, but this control can be undermined by male attempts to force copulations (Farr, 1989).

In a number of poeciliids no other male mating behaviour than thrusting is known (Farr, 1989). In other species of the family Poeciliidae, including the genus *Poecilia* there is size-based variation in male mating behaviour and small males never court. One such species is the sailfin molly, *P. latipinna* (Farr, 1980, 1989; Bisazza, 1993). In another species, the guppy, *P. reticulata* (Farr, 1980, 1989; Bisazza 1993; Houde, 1997) males may either court or attempt forced copulations. In guppies there is good evidence that females prefer courting males (Houde, 1997). In the sailfin molly several studies reported a preference for larger males, which court more often (Schlupp *et al.*, 1994; Ptacek & Travis, 1997; Witte & Ryan, 1998). Small males completely rely on attempting forced copulations (Parzefall, 1969; Travis &

Woodward, 1989). Many species of poeciliids are characterised by variation in male mating strategies. Some males, usually larger ones, court females, while others, usually smaller ones, attempt to force copulations.

Magurran & Seghers (1994) showed in a field experiment that female guppies pay a cost of male harassment as reduced feeding time, which results in decreased fecundity. Griffiths (1996) further corroborated this. That study compared feeding times of mixed sex and single sex groups of guppies and found that female guppies have less time to feed when males are present.

We investigated this phenomenon in the sailfin molly. We used a population which is part of an unusual mating system, in which a sexual species, the sailfin molly, serves as sperm-donor for an asexual species, the Amazon molly, *P. formosa* (for a review see Schlupp *et al.*, 1998). Amazon mollies are a gynogenetic hybrid species (Hubbs & Hubbs, 1932; Schlupp *et al.*, 1998) and form mixed shoals with their hosts in nature (Schlupp & Ryan, 1996).

In the present study we addressed the following questions: does sexual attention by *P. latipinna* males reduce feeding efficiency of females and how is this cost related to male body size?

## Methods

### *Fish*

All fish were collected from the San Marcos River, in Martindale (Caldwell County, Texas, USA) where both species have been introduced (Hubbs *et al.*, 1953). They were maintained in the laboratory in Austin and Hamburg in 20–200 l tanks at 25°C under 14/10 h artificial light conditions. They were fed daily ad libitum amounts of Tetra Min flake food and Tetra Tibs food tablets. The species were kept separate prior to the tests, but all fish had experienced both male and female *P. latipinna* and female *P. formosa* before being tested. After testing the fish were transferred to large outdoor tanks in the Brakenrigde Field Laboratory of the University of Texas.

### *Feeding tests*

Before each test a randomly selected focal female was isolated and not fed for 24 h to ensure that she was motivated to feed throughout the test. Each test consisted of three trials: in trial 1 a female was together with another *P. latipinna* female in the test tank (51 × 26 × 30 H cm), in trial 2 she was together with a *P. formosa* female, and in trial 3 she was together with a *P. latipinna* male. The order of the trials was random. Eleven of the trials were conducted in Austin, nine in Hamburg. Additional four tests were incomplete, only the trial with a male as partner could be scored. Those tests were only used in the regression analysis of male body size.

An overhead fluorescent light provided illumination with approx. 0.84 log lumen/m<sup>2</sup>. Ultraviolet radiation was absent.

To initiate a trial, the female was placed in the test tank and allowed to acclimate in a clear Plexiglas cylinder (8.2 cm diameter) with the respective partner present. After five minutes the cylinder was gently removed and the time the female spent feeding and the frequency of male copulatory attempts (or thrusting) and nipping was measured for five minutes. Nipping was defined as close contact of the male's mouth with the genital region of the female, thrusting as attempts of the male to introduce its gonopodium, a modified anal fin, into the female's genital opening (see Parzefall, 1969; Schlupp *et al.*, 1991).

The observers sat quietly about 1.0 m in front of the tank. The food item presented was a food tablet attached to a small Petri dish on the bottom of the tank. The food tablet was removed between tests and water in the tank was replaced daily. The fish were accustomed to food tablets before testing by feeding them tablets in their holding tanks. Feeding on the bottom is common in this species (pers. obs. IS). We recorded the following activities as feeding: feeding from the presented stationary food source, feeding from the surface of the water, the aquarium walls and bottom, or on floating matter in the water. All fish were measured after the trials and their standard length (SL) was recorded.

Each female was used as a test female only once, although she may have been used as a partner female in another test. Some males were used up to three times. In these cases we averaged the values of the tests and used those in our analysis. Thus each male contributed only one datum. We employed non-parametric statistics to analyse the data. All *p*-values are two-tailed.

## Results

*P. latipinna* females spent on average (median) 79.5 (144.1 interquartile range, IQR) seconds feeding accompanied by a conspecific female. Time increased when she was accompanied by an Amazon molly to 108 (73.9 IQR) seconds, but decreased to 58.5 (92 IQR) when accompanied by a male.

During the trials the test females appeared to be strongly interested in feeding. Feeding often occurred in bouts. If the partner was another female, feeding often occurred with the partner.

The time females spent feeding in the presence of a male was weakly positively correlated with male body size (Spearman rank correlation,  $\rho = 0.41$ ,  $z = 1.98$ ,  $N = 24$ ,  $p = 0.047$ ) (Fig. 1a), suggesting that smaller males impose a higher cost on females. Furthermore, male size was negatively correlated with the number of gonopodial thrusts (Spearman rank correlation,  $\rho = -0.48$ ,  $z = -2.41$ ,  $N = 24$ ,  $p = 0.016$ ) (Fig. 1b) and the number of nippings by males (Spearman rank correlation,  $\rho = -.58$ ,  $z = -2.81$ ,  $N = 24$ ,  $p = 0.005$ ) (Fig. 1c).

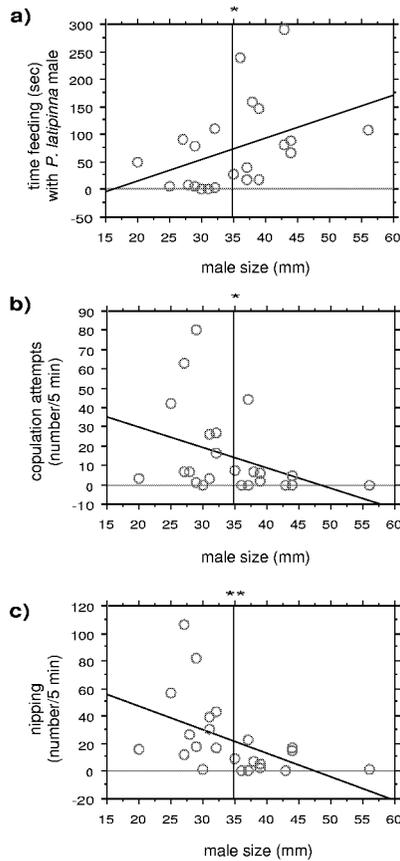


Fig. 1. Scattergrams of (a) male body size (mm) and the time females spend feeding, (b) male body size (mm) and number of copulatory thrusts, (c) male body size (mm) and number of nippings. The regression lines were determined using linear regression. \* refers to a  $p < 0.05$ , \*\* refers to a  $p < 0.01$ . See text for complete statistics.

To further analyse the effect of male body size we divided our sample into two groups, one group of males greater than median size (35 mm) and the other of males smaller than median size. For a completely independent sample of males from the same population ( $N = 86$ ) we found a median body size of  $34.6 (\pm 12.54 \text{ IQR})$  mm, indicating that the true population median for male body size is near 35 mm.

While the time females fed when accompanied by other females was essentially the same as when accompanied by large males (median = 85.5 (130.3 IQR); Friedman test,  $\chi^2 = 1.4$ ,  $p = 0.5$ ,  $N = 10$ ; Fig. 2), it dropped

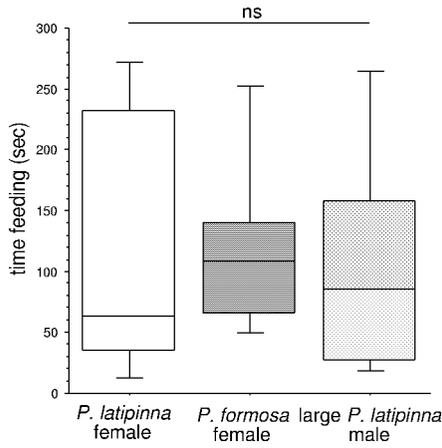


Fig. 2. Boxplots showing the time females spend feeding with one of three partners present. The males are large. ns = non significant.

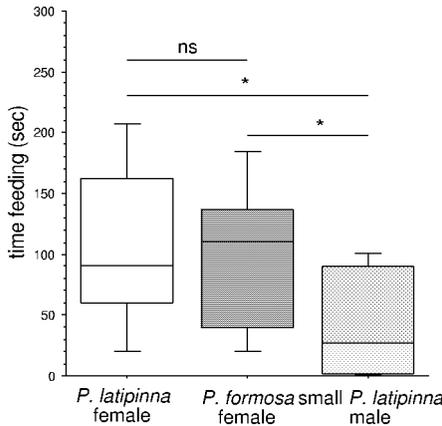


Fig. 3. Boxplots showing the time females spend feeding with one of three partners present. The males are small. \* refers to a  $p < 0.05$ , ns = non significant.

drastically when females were accompanied by small males (median = 27.5 (88 IQR); Friedman test,  $\chi^2 = 9.8$ ,  $p = 0.007$ ,  $N = 10$ ; Fig. 3). Pairwise post hoc Dunn's tests (Glantz, 1997) revealed that the time feeding with a male differed from time feeding with a conspecific female, and from the time with an Amazon molly (both  $p < 0.05$ ). The pairwise comparison of the time with an Amazon molly and a conspecific female was not significantly different.

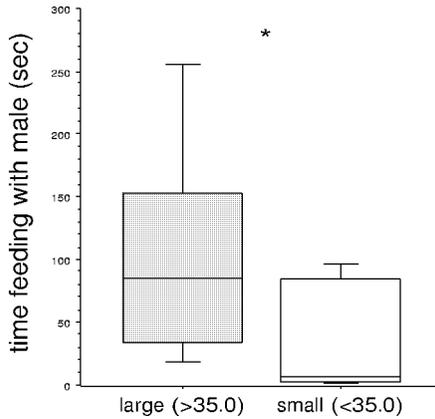


Fig. 4. Boxplots comparing the time females spend feeding with large and small males. \* refers to a  $p < 0.05$ .

The two groups of females with large and with small males differed significantly in the time females spent feeding (Mann Whitney  $U$ -test,  $z = -2.37$ ,  $p = 0.018$ ,  $N = 24$ ) (Fig. 4).

## Discussion

Our findings indicate that male attention reduces feeding time for females and induces a shift in female time allocation. More importantly, this cost differs with male body size.

If feeding time influences female body size, it might indirectly influence female fecundity, which is strongly correlated with female body size (Reznick & Miles, 1989 and unpublished data for *P. formosa*, IS).

Small males have a more severe effect on the female time budget, probably because they exclusively rely on forced copulations, a sneaky mating strategy. Thus the widespread female mating preference for large males may include a component of an adaptive avoidance of small, harassing males which might provide a direct benefit to the female. Possibly this pattern is more common than presently thought (see also Censky, 1997). In nature, females sometimes remain stationary, so that large males can monopolise access to them (pers. obs. IS). The benefit to the male is clear and the female may simply be trying to avoid harassment without having to flee.

This might also provide an adaptive explanation for the preference for larger males reported for Amazon mollies (Marler & Ryan, 1997). As Amazon molly females require only sperm, theoretically Amazon mollies can not receive any material or genetic benefit by preferring larger males. However, if females avoid harassment by consorting with larger males, they might benefit from a preference for larger males. Amazon molly females encounter a similar amount of male harassment, as do sailfin molly females (Schlupp *et al.*, in prep).

Magurran & Seghers (1994) argued that because female feeding time is directly linked to fecundity, any reduction of feeding time can be directly measured as cost. This has been shown convincingly for guppies (Hester, 1964; Reznik, 1983).

Feeding together with Amazon mollies does not seem to be different from feeding with conspecifics. This predicts that a sailfin molly female should not reject Amazon mollies to form mixed shoals. This corresponds with an earlier study on shoaling behaviour (Schlupp & Ryan, 1996).

In summary, we find that for sailfin molly females male harassment represents a potentially severe cost and that it is mainly small, thrusting males, that convey this cost.

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