

Male sexual harassment and female schooling behaviour in the eastern mosquitofish

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Among poeciliid fish, male sexual harassment is often intense and is costly for females. In *Gambusia holbrooki*, sexual harassment can greatly reduce female foraging efficiency when an isolated female is harassed by a single male and these costs are negatively correlated with male length. However, when females are in groups, male harassment is diluted and female foraging efficiency increases. When several males compete for the same female, mating attempts are monopolized by the dominant male and female foraging efficiency also increases. We tested whether females actively vary their schooling behaviour with conspecifics according to the presence of a harassing male. Consistent with the predictions, we found that females swam closer to each other when a male was visible. When chased by a male, females approached a group of males, and when males of different size were available, they preferred to stay close to large males. These results suggest that female schooling behaviour is a flexible strategy and that male sexual harassment may represent an important factor influencing social aggregation in poeciliids.

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Sexual conflicts arise when the mating strategy that maximizes the reproductive success of one sex is detrimental to the other sex (Parker 1979). A typical sexual conflict concerns the number of matings, since the optimal number of mates is usually larger for males than for females (Bateman 1948). As a consequence, male sexual harassment and coercive mating often evolve as male strategies to overcome the female's reluctance to mate, forcing her to accept matings that are potentially detrimental to her fitness (Clutton-Brock & Parker 1995). Females, on their side, are expected to adopt counter-strategies that reduce the occurrence of, or the costs associated with, unwanted matings, as observed across a wide taxonomic range (e.g. insects: Stone 1995; Muhlhauser & Blanckenhorn 2002; fish: Magurran & Seghers 1990; reptiles: Galan 2000; Shine et al. 2004; birds: Pizzari & Birkhead 2001; Persaud & Galef 2003; mammals: Smuts & Smuts 1993; Fox 2002).

Males of poeciliids, a group of internally fertilizing fish, are probably the most ardent males among vertebrates, their sexual activity being so intense that it can reach one

sexual act per min over the whole breeding season, which can last 6–12 months in tropical species (e.g. Bisazza et al. 1996; Houde 1997). Such intense sexual activity of males is costly to the female in terms of conspicuousness to predators (Magurran & Seghers 1994a; Pocklington & Dill 1995; Houde 1997) and foraging efficiency (Magurran & Seghers 1994b; Griffiths 1996; Schlupp et al. 2001; Pilastro et al. 2003). In the poeciliid eastern mosquitofish, *Gambusia holbrooki*, males do not court females and all copulations are achieved through gonopodial thrusting (Farr 1989; McPeck 1992; Bisazza 1993), a form of coercive mating tactic that is based on male inconspicuousness and manoeuvrability. Male sexual harassment significantly reduces the foraging efficiency of females in this species (Pilastro et al. 2003). This reduction is negatively correlated with male size, because small males are sexually more active (Pilastro et al. 1997). The foraging cost is mitigated, however, when the sex ratio is female-biased, as a result of the dilution of the harassment. Female foraging cost is also reduced in male-biased groups because small males are inhibited by the large, dominant male, which, in turn, has to devote some of his time to keeping the subordinate males far from the females (Bisazza & Marin 1995).

It is well known that female poeciliids adjust their schooling behaviour according to various ecological and social factors (e.g. Griffiths & Magurran 1997, 1998; Lachlan et al. 1998; Day et al. 2001; Evans et al. 2002;

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Croft et al. 2003). There are no empirical studies, however, on whether females adjust their schooling strategy to reduce the costs associated with male sexual harassment. In this study we experimentally tested three specific predictions about female schooling strategy in response to male sexual harassment. First, sexually unreceptive females are predicted to aggregate in a tighter school when a sexually active male is present. Second, unreceptive females should normally avoid males; however, if harassed by a male, females are predicted to approach other males, to promote male–male competition (Bisazza & Marin 1995; Pilastro et al. 2003). Third, if males of different size are visible, females are predicted to approach larger individuals.

METHODS

Study Species

Eastern mosquitofish, originally from North America, were introduced to Europe nearly a century ago and are now widely distributed throughout the Mediterranean countries. As in other poeciliids, male mosquitofish transfer sperm by inserting their modified anal fin, the gonopodium, into the female's genital pore (gonopodial thrusting, Constantz 1989). Such thrusts involve a male approaching a female from behind and trying to insert the gonopodium into her genital pore. The female can resist mating attempts by fleeing, changing orientation or lying against an object. In natural populations and in captivity, each male makes approximately one mating attempt per min (Bisazza & Marin 1995; Pilastro et al. 2003). Less than 1% of these attempts are successful and small males are more successful than large ones since they are both less conspicuous and manoeuvre better while they attempt to insert the gonopodium (Hughes 1985; Pilastro et al. 1997).

Fish Maintenance

The fish were collected with a hand net from Valle Averte, Venice lagoon, Italy. The research was authorized by the Istituto Superiore di Sanità and the fish were caught under a permit from the Regione Veneto. They were brought to the laboratory and maintained in mixed-sex groups (20–25 individuals at approximately 1:1 sex ratio) in several stock aquaria (150 litres, provided with natural gravel and an air filter) until they were used for the tests. Aquaria were provided with live plants (*Ceratophyllum*), illuminated by one 15-W fluorescent light and maintained at constant temperature ($25 \pm 1^\circ\text{C}$) and photoperiod (0600–2000 hours). Fish were fed twice a day with commercial food flakes and live *Artemia* nauplii and were fed to satiation before the trials. For the experiments we used sexually mature males and gravid, sexually unreceptive females. Each fish was used only once and at the end of the trial was put back into a postexperimental tank. No mortality was observed during the experiments and all fish were released back into the capture locality at the end of the experiments. The standard length ($\bar{X} \pm \text{SD}$) of the

whole fish was measured from the digital recordings of the experiments.

Experiment 1: Presence of Males

In this experiment we tested the hypothesis that females school closer to each other in the presence of a male. The experimental tank was a circular arena (diameter 65 cm) filled with 15 cm of water and uniformly illuminated with four 8-W fluorescent lamps (Fig. 1a). In the centre of the arena we positioned a Plexiglas transparent cylinder (diameter 19.5 cm, 16.5 cm high) containing a second plastic opaque cylinder (diameter 19 cm, 16.5 cm high), which was suspended on a monofilament line to a pulley system operated from a remote location that allowed us to move the opaque cylinder up and down. Two females, matched in size (standard length difference ≤ 1 mm), were put in the arena and allowed to settle overnight. The next morning, 30 min before the trial we put one male mosquitofish into the central cylinder. We could hide or show the male to the females by pulling down or up the opaque plastic cylinder, respectively. We tested 12 female pairs. As a control, a further six female pairs were presented with a female (instead of the male) in the central cylinder (total female pairs, $N = 18$).

Each trial consisted of eight observation periods, in four of which the stimulus fish in the central cylinder was visible and in four of which it was not. Observation periods lasted 30 min and were separated by 10-min intervals. Half of the trials started with the stimulus fish visible in the central cylinder and half with the stimulus fish kept hidden from the schooling females. A video camera, positioned about 2 m above the centre of the apparatus, was used to videorecord the trials. Video recordings were subsequently digitalized. We examined 3 frames/min and by means of a computer program we took two measures of the distance between the two females: (1) the angle obtained by virtually connecting the heads of the two females with the centre of the apparatus and (2) the linear distance between the two females (Fig. 1b). We transferred the calculated values to a spreadsheet file. In total, we obtained 720 distance measurements for each trial (360 with the stimulus fish visible to the two experimental females and 360 with the stimulus fish not visible). From these measures we calculated the mean angle and the mean distance between the two experimental females for each 30-min period.

Experiment 2: Preference for Other Males

Our aim in this experiment was to test whether a female actively approaches a group of males when she is harassed by a single male. The experimental apparatus (Fig. 2a) consisted of two adjacent tanks (40×60 cm and 36 cm high, and 30×60 cm and 36 cm high). The first tank (subject chamber) contained a net of 2×2 mm in a plastic frame of 25×36 cm, attached to the back of the subject chamber. This net wall partially divided the subject chamber in half and allowed the test female to swim from

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