

Social preferences based on sexual attractiveness: a female strategy to reduce male sexual attention

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Male sexual harassment of females is common across sexually reproducing species and can result in fitness costs to females. We hypothesized that females can reduce unwanted male attention by constructing a social niche where their female associates are more sexually attractive than themselves, thus influencing the decision-making of males to their advantage. We tested this hypothesis in the Trinidadian guppy (*Poecilia reticulata*), a species with high levels of male sexual harassment. First, we confirmed that non-receptive females were harassed less when they were paired with a more sexually attractive (receptive) female than with another non-receptive female. We then found that, indeed, females exploit this as a strategy to reduce sexual harassment; non-receptive females actively preferred to associate with receptive over non-receptive females. Importantly, when given access only to chemosensory cues, non-receptive females still showed this preference, suggesting that they use information from chemical cues to assess the sexual attractiveness of potential female partners. Receptive females in contrast showed no such preferences. Our results demonstrate that females can decrease male harassment by associating with females that are more sexually attractive than themselves and that they perform active partner choices based on this relative attractiveness. We propose that this strategy is likely to represent an important pathway by which females can construct social niches that influence the decision-making of others to their advantage; in this case, to reduce the sexual harassment they experience.

Keywords: sexual conflict; sexual harassment; social structure; chemosensory reproductive cues; *Poecilia reticulata*

1. INTRODUCTION

Conflict between males and females over optimal mating rate [1,2] can result in sexual harassment, a type of sexual coercion that often takes the form of males pursuing, courting and repeatedly attempting to mate with females [3]. Females have evolved traits to counter male coercion that are morphological [4,5], physiological [6] and behavioural [7–9]. Importantly, evidence is now emerging from a number of taxa that females employ social strategies in their attempt to reduce male harassment [7,10,11], suggesting that male sexually coercive behaviour has a strong selective force on sociality in sexually reproducing species. However, in contrast to morphological counter adaptations (see [1] for a review), we know relatively little about how social counter strategies directly influence the level of sexual harassment that females experience and to what degree females actively employ these strategies.

In many species, social associations are dynamic, with individuals benefiting from changing social partners as they weigh the costs and benefits related to key behaviours such as foraging, predator avoidance and reproduction

[12]. As such, there is potential for individuals to construct a social niche that will work to their advantage. This advantage may come in the form of an individual constructing a niche that influences the decisions made by conspecifics in a way that benefits that individual. For example, recent work has demonstrated that males will associate with less sexually attractive males to influence the choices of females and increase their own reproductive success [13,14]. We hypothesize that females can likewise construct a social niche based on sexual attractiveness that will influence the decision-making of males, but in this case, to reduce sexual attention. We predict that females that are not interested in mating (anoestrous or otherwise non-receptive) can reduce the amount of attention they receive from males in a group by actively associating with females that are more sexually attractive than themselves (in oestrous or otherwise receptive). We test this hypothesis using the Trinidadian guppy (*Poecilia reticulata*) and investigate the mechanisms that may underpin such a strategy.

The Trinidadian guppy is a small freshwater fish that breeds continuously and has a promiscuous mating system [15]. It lives in fission–fusion societies, where females form small shoals that are continuously investigated by males that move from shoal to shoal looking for mates [16,17]. Female guppies are highly receptive

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to male sexual behaviour when they are virgins and several days each month just after parturition [18], at which time they emit chemical cues that attract males and stimulate male sexual activity [19]. For the remainder of the time, females are generally not receptive to mating attempts, although insemination at this time can lead to successful fertilization via sperm storage [20,21]. Males, therefore, exhibit high levels of coercive behaviour in the form of harassment of females for mating opportunities and forced copulations [15,22]. This leads to reduced energy intake [23,24] and fecundity [25] in females, and they would benefit from being able to actively reduce the amount of harassment that they receive during non-receptive periods.

We predict that female guppies can reduce male attention by making association decisions based on social partner attractiveness; that is, given that they will encounter males on a regular basis [16], they can reduce the male attention they receive by choosing to partner with the more sexually attractive, receptive females in the shoal. We expect that non-receptive females will show a strong preference for receptive social partners, but that this preference will be weaker, or perhaps even absent, in receptive females as they show interest in male sexual behaviour and therefore are not likely to be attempting to reduce male attention [18]. By including receptive females as focal individuals in our choice experiments, we have a powerful control to aid in our interpretation of the results. Importantly, we test for preferences based specifically on reproductive chemosensory cues (which are used by males to locate sexually receptive females [19]), which allows us to look at preferences based directly on sexual receptivity as opposed to other characteristics of females that may differ when they are receptive and non-receptive (e.g. behavioural or morphological differences).

2. MATERIAL AND METHODS

For all three experiments, we used captive-reared Trinidadian guppies descended from wild fish caught in the Aripo River in the Northern Mountain Range, Trinidad (10°40' N, 61°14' W) in 2008. All experimental fish were kept in full spectrum light on a 12 L:12 D cycle and fed commercial fish flake food once a day. All data analysis was carried out in PASW Statistics 18 (IBM Corp., Somers, NY, USA).

(a) *Experiment I: do non-receptive females experience reduced sexual harassment when associating with a more sexually attractive (receptive) social partner?*

We quantified the amount of time a male guppy spent in proximity to a focal female in a non-receptive reproductive state in one of two treatments: (i) when she was with a receptive female partner ($n = 10$) and (ii) when she was with a non-receptive female partner ($n = 10$). Receptive females were females that had given birth within the last 3 days prior to testing [18], while non-receptive females were in the middle or the end of their gestation cycle. Test and stimulus females were isolated for a period of 3 to 10 days prior to the experiment to monitor their reproductive state (see electronic supplementary material). Females used in the same trial had been isolated for an equal amount of time and were matched in body length (to ± 1.5 mm). Males were

isolated from females prior to testing (3–10 days) in order to increase their interest in females. Each fish was used in only one trial.

Testing took place in a 59 × 29 cm tank (15 cm water depth). Perforated dividers created three equal-sized compartments, and focal and stimulus females were placed in the two end zones and the male in the middle zone. The fish were allowed 5 min settling time, after which the dividers were lifted, so all fish could swim freely in the entire tank for the duration of the data collection. During the following 10 min, the time for which the male was within two body lengths of the focal female was recorded. We tested for an effect of treatment on the amount of time the males spent in proximity to the focal females using an independent samples *t*-test.

(b) *Experiment II: do females actively prefer to associate with receptive or non-receptive female social partners?*

Using a binary choice test, the time receptive and non-receptive focal females spent associating with a receptive versus a non-receptive stimulus female was recorded over a 10 min period (see above for a definition of receptive and non-receptive). Test and stimulus females were isolated for a period of 3 to 8 days prior to the experiment to monitor their reproductive state (see electronic supplementary material). Females used in the same trial had been isolated for an equal amount of time and were matched in body length (to ± 1.5 mm).

Stimulus fish were contained in 7 cm diameter perforated, transparent cylinders at either end of a 59 × 29 cm tank test tank (15 cm water depth). They were placed in the tank first and the focal female was then released into the centre of the tank. Each trial commenced after a 5 min settling period. A focal female was defined as associating with a stimulus female if she was within 5 cm of the cylinder.

We tested for a difference between test groups in the responsiveness to the stimulus fish (total amount of time spent associating) using an independent samples *t*-test. For both test groups, we used one-sample *t*-tests to test for a difference between the proportion of the total association time that females spent associating with the receptive female and the proportion expected assuming no stimulus fish preference (50%). Proportions were *arcsine*-square root-transformed to meet assumptions of normality.

(c) *Experiment III: do females use chemosensory cues to assess receptivity of social partners?*

Using a binary choice test, receptive and non-receptive females (as defined above) were given the choice between occupying zones with water containing chemosensory cues from receptive and non-receptive females, respectively (see electronic supplementary material). Test females were housed in group tanks for a period of 2–22 days prior to the experiment to monitor their reproductive state (see electronic supplementary material). Each non-receptive focal female was matched in size (to ± 1.5 mm) and the length of time housed in the group tank to a receptive focal female tested on the same day.

Trials were carried out in a 33 × 25 cm tank. Above each tank end was placed a funnel for stimulus water input (175 ml), connected to tubing going into the tank and terminating 5 cm above the bottom (see electronic supplementary material). Flow rates of input water were adjusted to

10 ml min⁻¹ with flow rate meters (MMA-35, Dwyer Instruments, Michigan City, IN, USA). The tank was divided into three equally sized zones by vertical lines drawn on the front side; a left and right 'choice zone' and a central 'neutral zone'. A similar experimental set-up has been used by other researchers for chemosensory cue choice tests with *P. reticulata* [19,26] and other fish species [27,28].

The focal fish was placed in the middle of the test tank and allowed to settle for a 40 min period after which the flow rate meter valves were opened and stimulus water was allowed to flow into the tank for the remainder of the trial. Stimulus water from a receptive female was introduced in one choice zone and stimulus water from a non-receptive female was introduced in the other. The end of the tank to receive each stimulus type was balanced across trials. The time the focal fish spent in each zone was recorded during a 10 min observation period following the introduction of the stimulus water. Data collection began when the fish was swimming normally again after the interruption (which it usually did within 1 min). Trials in which the focal fish did not visit both choice zones were discarded.

The data did not meet a normal distribution, so non-parametric statistics were applied. We tested for a difference between test groups in responsiveness to stimulus water (amount of time spent in the choice zones) using an independent samples median test. For each test group, we used a Friedman test and *post hoc* Dunn test [29] to test for differences in the proportion of time females spent in the three zones (the two choice zones and the neutral zone).

3. RESULTS

(a) *Experiment I: do non-receptive females experience reduced sexual harassment when associating with a more sexually attractive (receptive) social partner?*

The amount of time males spent in proximity to non-receptive focal females differed significantly between the two treatments ($t_{18} = 5.070$, $p < 0.0001$). Females partnered with a receptive female received less male attention than females partnered with a non-receptive female (figure 1).

(b) *Experiment II: do females actively prefer to associate with receptive or non-receptive social partners?*

Receptive and non-receptive females did not differ in the amount of time they spent associating with the stimulus fish ($t_{18} = 1.344$, $p = 0.196$). However, non-receptive females showed a significant preference for associating with receptive females ($t_9 = 6.694$, $p < 0.0001$), while receptive females did not exhibit any preference ($t_9 = 0.855$, $p = 0.415$; figure 2).

(c) *Experiment III: do females use chemosensory cues to assess receptivity of social partners?*

Receptive and non-receptive females did not differ in their responsiveness to the stimulus water ($n = 24$, $p = 0.220$). However, non-receptive females showed a significant zone preference ($n = 12$, $\chi^2 = 8.667$, $p = 0.013$) and *post hoc* tests revealed that this was due to a preference for associating with chemosensory cues from receptive females (receptive versus non-receptive: positive contrast, $z = 2.53$, $p < 0.05$; receptive versus neutral: positive

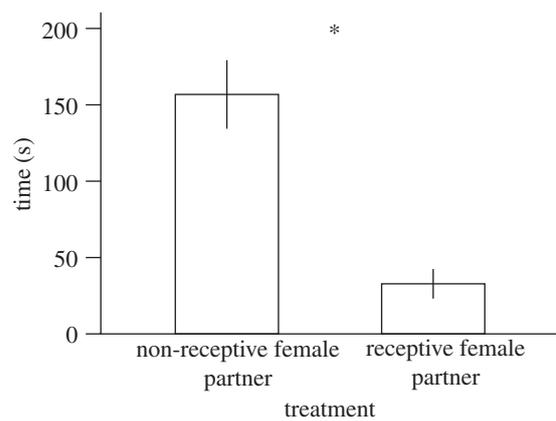


Figure 1. Average amount of time male Trinidadian guppies spent in proximity to a non-receptive focal female over a 10 min period when the focal female was paired with either a non-receptive (equally sexually attractive) or receptive (more sexually attractive) female partner (error bars: ± 1 s.e.m.; asterisk indicates significant difference between groups ($p < 0.0001$)).

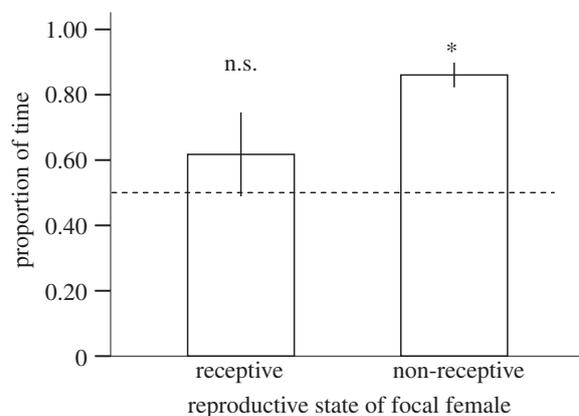


Figure 2. Average proportion of association time receptive and non-receptive female Trinidadian guppies spent associating with a receptive and a non-receptive female partner (error bars: ± 1 s.e.m.; n.s., not significantly different from 0.5 ($p > 0.05$); asterisk indicates significantly different from 0.5 ($p < 0.0001$)).

contrast, $z = 2.55$, $p < 0.05$; non-receptive versus neutral: zero contrast, $z = 2.09$, $p > 0.05$; d.f. = 33), while receptive females did not exhibit any preference ($n = 12$, $\chi^2 = 2.167$, $p = 0.338$; figure 3).

4. DISCUSSION

Our findings provide direct support for the hypothesis that females can reduce levels of sexual harassment by actively selecting social partners that are relatively more attractive to males; that is, by positioning themselves in a social niche that influences the decision-making of others to their advantage. Female guppies not in a receptive reproductive state received significantly less male attention when they were partnered with a receptive (and thereby more attractive) female than when they were partnered with another non-receptive female. Furthermore, non-receptive females actively preferred to associate with receptive females, while receptive females

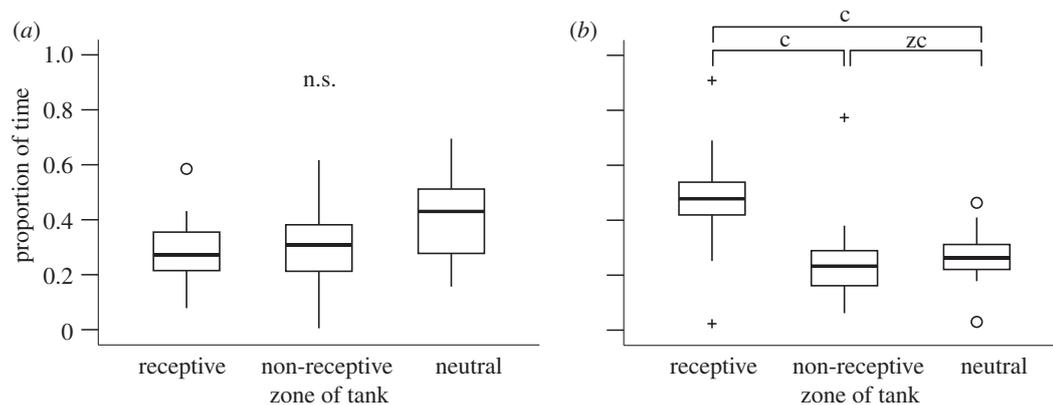


Figure 3. Median box-plots with inter-quartile range of proportion of observation time (a) receptive and (b) non-receptive female Trinidadian guppies spent in each zone of a test tank with chemosensory cues from a receptive female (receptive zone) and a non-receptive female (non-receptive zone) separated by a central, neutral zone (see text; 'c', contrast detected with *post hoc* Dunn test; 'zc', zero contrast detected with *post hoc* Dunn test; 'n.s.', no overall significant difference among groups ($p > 0.05$)).

did not exhibit any preference for social partners based on their reproductive state. Importantly, this preference was also present in non-receptive (but not in receptive) females when they only had access to chemosensory information, suggesting that they use these cues in their assessment of the sexual attractiveness of potential social partners, and that it was the reproductive state and not some other aspect of a female that was responsible for the preferences seen with live social partners.

Social association preferences allow animals to change the social landscape in which behaviours are performed and ultimately, upon which selection acts [30,31]. There is now evidence that individuals can construct a social niche that increases their competitiveness in acquiring mates. For example, in a recent study, Oh & Badyaev [14] found that sexual attractiveness to females drives association patterns in male house finches (*Carpodacus mexicanus*), with males that scored low in attractiveness actively associating with males that were even less attractive, thus increasing the former's reproductive success. Evidence for this type of assortment strategy in males has also recently been reported in forked fungus beetles (*Bolitotherus cornutus*) [13]. Our results show that females can use a similar strategy, associating with individuals based on sexual attractiveness, but in this case, reducing their attractiveness to males (and thereby male harassment) by choosing social partners within a shoal that are more attractive than themselves. In guppies, shoal composition is very dynamic, with males joining and leaving shoals on a time scale of seconds [16]. Under these conditions, females are not able to avoid encounters with males and males will harass both receptive and non-receptive females. Our results demonstrate that non-receptive females preferentially associate with receptive females and in doing so receive less harassment from those males than they would if they were associated with non-receptive females. One of the major factors influencing social decisions in animals is predation risk, with individuals forming social groupings that minimize their individual risk of predation [12]. The results of this study however, cannot be explained by individuals attempting to reduce their risk of predation. If predation risk were driving social preferences in females based on receptivity, we would actually predict the opposite to

the observed patterns. That is, all females would choose partners that were either more attractive to predators than themselves (e.g. 'fatter' and 'slower' in the case of females that have not recently given birth (i.e. are non-receptive)) [32] or that were more morphologically similar to reduce the oddity effect [33–35]. We did not find support for either of these.

Changes in social association patterns as a means of minimizing sexual harassment and coercion have been found in other species. In the Eastern mosquitofish (*Gambusia holbrooki*), a poeciliid species with a high level of male sexual harassment, females preferably approach larger shoals and larger female individuals, but only when a male is present, indicating that these shoaling decisions function to minimize harassment [36]. In Grevy's zebra (*Equus grevyi*), females are more prone to harassment when they lactate, and it has been found that lactating females spend more time with their primary male associate than non-lactating females [11]. This reduces the amount of harassment they experience because female zebras are less harassed by males to which they have a strong social bond. In several primate species, females associate and mate with specific male companions, who in turn protect them from harassment and coercion from other males [37]. Understanding how such individual strategies scale up to the level of the population and influence the dynamics and the structure of the population social network and the evolutionary implications of such effects provides an exciting and challenging area for future work.

Receptive females in our study did not exhibit the preferences found in non-receptive females. This supports our assumption that receptive females do not have a strong incentive to reduce male attention. Of course, we cannot exclude the possibility that receptive females were not able to detect chemical cues on reproductive state and thus did not show a preference in either of the choice experiments. Hormonal influences on olfactory sensitivity have been documented across vertebrate taxa [38–40] and it could be that in guppies, receptive females cannot easily detect the reproductive chemosensory cues of other receptive females. The receptive females did not, however, differ from non-receptive females in their responsiveness to the testing situation. Further investigation

into the mechanism and function behind differences in behaviour would be gainful.

Our findings demonstrate that adaptive social partner choice is not only based on the direct benefits individuals can provide. Social partners also act as the background against which the traits of individuals are judged (e.g. their attractiveness), and this has implications for how they are treated by others. The behavioural strategy investigated here is an example of how individuals take this into account in their social partner decisions, in a sexual conflict setting. The results underline that female responses to sexual harassment can have profound consequences for social structure [41,42]. Association decisions based on sexual attractiveness may well be widespread in other species with high levels of harassment. Our study thus helps to elucidate the relationship between sexual conflict and social structure, a relationship that may be central to our understanding of the evolution of sociality.

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