Male sexual harassment alters female social behaviour towards other females

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Male harassment of females to gain mating opportunities is a consequence of an evolutionary conflict of interest between the sexes over reproduction and is common among sexually reproducing species. Male Trinidadian guppies *Poecilia reticulata* spend a large proportion of their time harassing females for copulations and their presence in female social groups has been shown to disrupt female–female social networks and the propensity for females to develop social recognition based on familiarity. In this study, we investigate the behavioural mechanisms that may lead to this disruption of female sociality. Using two experiments, we test the hypothesis that male presence will directly affect social behaviours expressed by females towards other females in the population. In experiment one, we tested for an effect of male presence on female shoaling behaviour and found that, in the presence of a free-swimming male guppy, females spent shorter amounts of time with other females than when in the presence of a free-swimming female guppy. In experiment two, we tested for an effect of male presence on the incidence of aggressive behaviour among female guppies. When males were present in a shoal, females exhibited increased levels of overall aggression towards other females compared with female only shoals. Our work provides direct evidence that the presence of sexually harassing males alters female–female social behaviour, an effect that we expect will be recurrent across taxonomic groups.

Key words: *Poecilia reticulata*; sexual harassment; sexual conflict; social behaviour; shoaling; aggression

1. INTRODUCTION

Sexual conflict arises from contrasting interests between males and females concerning reproduction [1]. In a number of species, one outcome of sexual conflict is male harassment of females for sexual contact and coercion of females into mating [2]. There is ample evidence that male sexual harassment of females can lead to females altering their behaviour in an attempt to resist male sexual advances and reduce levels of harassment, for example [3]. In addition, it is increasingly becoming apparent that the presence of sexually harassing males directly affects female social behaviour [4–8]. In a recent study, Darden *et al.* [6] found that male sexual behaviour may in fact be detrimental to female sociality, with female Trinidadian guppies (*Poecilia reticulata*) showing fragmentation of social networks and a decreased propensity to develop social recognition based on familiarity with other females in their environment. There is suggestive evidence in mammals that harassing males affect fitness–fusion properties of groups of females [3] and female–female levels of aggression [9]. These are perhaps the most obvious routes by which male sexual behaviour can disrupt female social network structure and the development of social recognition; however, these effects have not been explored experimentally.

We present an experimental study investigating to what degree the presence of harassing males directly influences the nature of female–female social interactions. We examined this in Trinidadian guppies, a species in which males spend a large proportion of their time pursuing females for copulation while performing courtship displays and gonopodial thrusting [10]. Given the documented effect of male harassment behaviour on female movement and activity patterns in a number of species, for example [3,11], we expect that females will increase their mobility in the presence of harassing males, leading to a decrease in the amount of time a female will spend with an individual shoal in an attempt to avoid male attention. Furthermore, we expect the levels of female–female aggression to increase in the presence of harassing males. In their attempt to deter males, females of several species will behave aggressively to approaching males [12–14] and we predict that a heightened level of aggression in the presence of males will carry over into female–female interactions.

2. MATERIAL AND METHODS

Laboratory-reared Trinidadian guppies descended from wild-caught fish from the Aripo River in the Northern Mountain range of Trinidad (10°39′ N, 61°13′ W) were used in this study. We performed two experiments using average-sized (20–25 mm) females as focal individuals and average-sized males and small females (15–18 mm) as stimulus fish. In the first experiment, we recorded focal female shoaling behaviour (time spent within 5 cm of a stimulus shoal) during a 10 min observation period in a 60 × 60 cm tank containing three equidistant two-female stimulus shoals restrained in transparent cylinders (9.5 cm diameter) to maintain their spatial position. Trials started after an initial 30 min acclimatization period with the focal female swimming freely in the test tank and a subsequent 5 min period after the addition of either a male (male treatment) or small (male-sized) female (female treatment) guppy. We tested for an effect of treatment on the amount of time that focal females spent shoaling with stimulus shoals using a multi-variate general linear model (GLM). We used a Wilcoxon signed-rank test to test for a difference in the number of fission events initiated by the focal female and the free-swimming stimulus fish in each treatment. In our second experiment, we measured levels of aggression exhibited by average-sized females in all-female groups (female treatment: three average-sized focal females plus three small females) and in mixed-sex groups (male treatment: three average-sized focal females plus three males) at an experimentally provided food patch (microscope slide with fish flake attached with petroleum jelly). Fish were observed over a 15 min period, beginning when the first fish made contact with the foraging patch, and the actor and recipient of six well-defined aggressive behaviours (nips, nudges, chase, parallel swimming, tail beating and patch dominance [15]) were recorded. We tested for an effect of treatment on the amount of aggressive behaviour exhibited by focal females (i) overall and (ii) towards other average-sized females using a GLM. All tests were conducted in SPSS v. 17.0.

3. RESULTS

(a) The effect of males on shoaling behaviour in females

Treatment had a significant effect on female shoaling behaviour (multi-variate GLM: \( F_{2,27} = 4.283,\)
GLM: We found a significant effect of male presence on females foraging at a food patch if males were present than if presence of males. Secondly, females behaved more likelihood to be the initiators of fission events in the male treatment ($n = 15$) or a free-swimming male ($n = 15$; bars represent standard error). The post hoc univariate analyses revealed that in the presence of a free-swimming stimulus male, females spent less time shoaling with the stimulus shoals overall ($F_{1,28} = 5.187$, $p = 0.031$) and had shorter shoaling bouts with individual shoals ($F_{1,28} = 6.762$, $p = 0.015$) compared with when they were in the presence of a free-swimming stimulus female (figure 1a). When shoal fission occurred in the presence of a free-swimming stimulus fish (i.e. focal and stimulus fish were in the same shoaling zone), this was more likely to be initiated by the focal female than the free-swimming stimulus fish in the male treatment ($n = 13$, $Z = -2.335$, $p = 0.020$), but not in the female treatment ($n = 10$, $Z = -0.548$, $p = 0.584$; figure 1b).

(b) The effect of males on aggression among females

We found a significant effect of male presence on aggressive behaviour in focal females (multi-variate GLM: $F_{2,27} = 5.513$, $p = 0.010$, figure 2) with more aggression overall being exhibited by focal females in the presence of males ($F_{1,28} = 9.572$, $p = 0.004$, figure 2a) and with more aggression directed specifically towards other females of similar size in the presence of males ($F_{1,28} = 5.826$, $p = 0.023$, figure 2b) compared with when males were absent.

4. DISCUSSION

We found that female social interactions are strongly affected by the presence of harassing males. Firstly, when females were in the company of a male, they showed a reduction in the amount of time they spent shoaling with conspecific females. This is an indication that females showed increased mobility and an alteration in space use in the male treatment. The most likely explanation is that they are attempting to avoid male attention by moving to a different shoal or area of the habitat [16,17], as supported by their greater likelihood to be the initiators of fission events in the presence of males. Secondly, females behaved more aggressively towards other females in a group while foraging at a food patch if males were present than if males were not present. In fact, heightened aggression levels exhibited by females overall towards conspecifics when there were males in the group strongly suggests that aggression towards males is re-directed or carried over to other females in the presence of males. One mechanism for this could be an effect of males on circulating hormone levels in females [18].

Effects on female sociality are likely to occur across a range of taxa where males harass females for mating opportunities and coerce females into mating with them. In fact, in social animals, sexual coercion may have its main impact on females because of its potential to disrupt the dynamics of social interactions, as shown in this and other studies [3,6,9]. In socially grouping species, affiliative and agonistic behaviours are central to the maintenance of group structure and collective group behaviour [19]. Types and levels of aggression often depend on the strength and nature of social bonds and on the successful establishment of dominance hierarchies [20,21]. Furthermore, as recent studies have demonstrated, the nature and the strength of social relationships that a female has with

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Figure 1. (a) Average time female Trinidadian guppies spent shoaling with all female shoals (white bars) and average time females spent with a single shoal before swimming away (black bars) in the presence of either a free-swimming female ($n = 15$) or a free-swimming male ($n = 15$; bars represent interquartile range). (b) Median number of shoal fission events initiated by focal female guppies (white bars) and either free-swimming stimulus females ($n = 10$; female treatment) or males ($n = 13$; male treatment; bars represent interquartile range).

Figure 2. Average number of aggressive events exhibited by average-sized female Trinidadian guppies towards other average-sized females in the group (white bars) and towards all other conspecifics in a group (black bars), while foraging at a food patch in the absence ($n = 15$; female treatment) and presence ($n = 15$; male treatment) of males.
other females in the population can have direct fitness consequences [22–24]. We would thus expect the impact that male harassment has on female social behaviour to be a strong evolutionary driving force.

In conclusion, the results presented here provide unique insight into the consequences of male sexual behaviour for social interactions in females. Our results strongly suggest that male harassment behaviour has a strong impact on the nature of inter-individual female interactions and behaviours expressed at the level of groups and even populations. Furthermore, we suspect that these effects are widespread and represent a neglected consequence of male sexual harassment across taxonomic groups; testing this prediction provides an exciting challenge for future research.

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