

1 **Social implications of the battle of the sexes: sexual harassment disrupts female**
2 **sociality and social recognition**

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15

1 **Abstract:**

2 Across sexually reproducing species males and females are in conflict over the control of
3 reproduction. At the heart of this conflict in a number of taxa is male harassment of
4 females for mating opportunities and female strategies to avoid this harassment. One
5 neglected consequence that may result from sexual harassment is the disruption of
6 important social associations. Here we experimentally manipulate the degree of sexual
7 harassment that wild female guppies (*Poecilia reticulata*) experience by establishing
8 replicated, semi-natural pools with different population sex ratios. We quantify the effects
9 of sexual harassment on female social structure and the development of social recognition
10 among females. When exposed to sexual harassment we found that females had more
11 disparate social networks with limited repeated interactions when compared to females
12 that did not experience male harassment. Furthermore, females that did not experience
13 harassment developed social recognition with familiar individuals over an eight-day
14 period whereas females that experienced harassment did not, an effect we suggest is due
15 to disruption of association patterns. These results show that social network structure and
16 social recognition can be affected by sexual harassment, an effect that will be relevant
17 across taxonomic groups and that we predict will have fitness consequences for females.

18

19 Key words: familiarity, *Poecilia reticulata*, sexual conflict, sexual harassment, social
20 network, social recognition

21

1 **Introduction**

2 Sexual conflict, where males and females differ in their reproductive interests, is
3 widespread across sexually reproducing species (Arnqvist & Rowe 2005). This conflict is
4 rooted in male reproductive success generally being limited by their access to females
5 while female reproductive success is often dependent on the availability of energetic
6 resources for offspring production (Emlen & Oring 1977). A resultant conflict over the
7 outcome of male-female interactions can thus develop such that the optimal reproductive
8 scenario is different for males and females (Chapman 2006) and we see the development
9 of behaviours and adaptations that can benefit one sex whilst being costly to the other
10 (Moore et al. 2003). Central to recognizing and understanding sexual conflict and its
11 implications for evolutionary processes such as sexual selection and sexually antagonistic
12 coevolution, is a thorough analysis of the costs females incur from male mating strategies
13 (Arnqvist & Rowe 2005; Hosken & Stockley 2005).

14

15 Sexual harassment, i.e. repeated male coercion of females to obtain a mating (Clutton-
16 Brock & Parker 1995) promotes sexual conflict because of the asymmetry in costs to
17 males and females. Well examined costs to females of sexual harassment include,
18 energetic costs (Clutton-Brock & Langley 1997), increased predation risk (Rowe 1994),
19 reduced feeding opportunities (Magurran & Seghers 1994a) and physical injury
20 (Blanckenhorn et al. 2002). Such costs may decrease female lifetime fitness and increase
21 mortality (Meader & Gilburn 2008; Sakurai & Kasuya 2008) and selection has resulted in
22 females developing a number of strategies to reduce their exposure to male harassment.
23 For example, females may avoid habitats that contain high densities of males (Darden &

1 Croft 2008), form alliances to defend themselves from male attacks (Silk 2007b) or
2 accept advances from males where resistance would otherwise likely result in death or
3 injury (Mesnick & Leboeuf 1991). A continued conflict between the sexes thus exists,
4 which is a profound evolutionary driving force (Chapman *et al.* 2003).

5

6 One as of yet neglected consequence that may result from sexual harassment is the
7 disruption of important social associations due to the presence of harassing males and
8 female avoidance strategies. Social animals are often inter-connected into complex
9 heterogeneous social networks (Croft *et al.* 2008) and the structure of social networks can
10 have important fitness implications for individuals as it sets the stage for key behaviours
11 such as foraging, mating and antipredator behaviour (Krause *et al.* 2007). If male sexual
12 harassment disrupts female social structure it may lead to fitness costs for females (Silk
13 2007b; Silk 2007a). Previous work has demonstrated that sexual harassment can
14 influence female habitat use, activity and movement patterns across a range of taxa
15 (Trillmich & Trillmich 1984; Krupa *et al.* 1990; Stone 1995; Darden & Croft 2008). For
16 example, in Grevy's zebra (*Equus grevyi*) rates of female movement are increased with
17 increased sexual harassment (Sundaresan *et al.* 2007). As a result one can hypothesize
18 that female avoidance strategies in response to male sexual harassment will influence
19 female-female social network structure by, for example, breaking female-female social
20 ties and generating more dispersed female-female social networks (i.e. fewer connections
21 between females). A disruption of female social ties could conceivably have implications
22 for the opportunity for females to develop social familiarity and social recognition where
23 repeated or prolonged encounters are required for recognition to develop (see Griffiths &

1 Ward 2006; Ligout & Porter 2006 for reviews). Whilst there is growing interest in social
2 components of fitness (Silk 2007a; Silk 2007b) and the mechanisms underpinning social
3 networks in animals (Croft et al. 2008), the potential effect and implications of sexual
4 harassment on female social structure remains unknown.

5

6 Here we examine directly how males in a population influence female social network
7 structure and how this in turn influences the development of social recognition among
8 females. We use the Trinidadian guppy, *Poecilia reticulata*, a species of small freshwater
9 fish where we see extremely high levels of male harassment of females (Magurran 2005),
10 as a model system. In this species males spend the majority of their time in pursuit of
11 females, employing both courtship and forced or coerced mating tactics (Magurran 2005).
12 Previous research has documented high energetic costs of harassment to females, as
13 indicated by decreased foraging opportunities (Magurran & Seghers 1994a), and females
14 are known to employ a number of behaviours to reduce this harassment, including fleeing
15 from harassing males (Magurran & Seghers 1994b) and occupying habitats that contain a
16 low density of males such as areas of high predation risk (Croft et al. 2006b; Darden &
17 Croft 2008). Social familiarity is known to be important in structuring guppy social
18 networks (Croft et al. 2004; Croft et al. 2006a) and they are capable of individual
19 recognition (Ward et al. 2009). Under laboratory conditions familiarity among females
20 can take up to twelve days to develop, suggesting that repeated encounters are important
21 for the development of social recognition in this species (Griffiths & Magurran 1997).

22

1 We undertake two experiments in which we establish replicated populations of fish in
2 semi-natural pools under two different sex ratios. In the first experiment we collect
3 information on patterns of social association between all fish in the population and use
4 social network analysis to quantify the population social fine structure (Croft et al. 2008).
5 We then compare this structure between populations that have experienced different sex
6 ratios and quantify the effect of males on female-female social structure. In the second
7 experiment we quantify the effect of males on the development of female-female social
8 familiarity by recording shoaling preferences by females for others from the same or a
9 different population over a twelve-day period, testing the hypothesis that males will
10 disrupt the opportunity for females to develop social recognition.

11

12 *Materials and Methods*

13

14 *Study population*

15

16 The study was carried out using wild-caught guppies from the lower portion of the Turure
17 River (10°40'20" N 61°09'60" W) in the Northern Mountain Range Trinidad from May-
18 June 2007 and April-May 2008. Adult male and female guppies were caught in two-
19 metre seine nets from pools in the river spaced over a distance of 400 m and individually
20 marked using visual implant elastomer (Croft *et al.* 2003). All experiments were carried
21 out in outdoor semi-natural pools (180 cm diameter, algae coated substrate from the river
22 of origin; aged tap water 14 cm deep).

23

1 *The effect of males on female social network structure*

2 For each replicate, 8 large females were placed in an experimental pool (N=12) on Day 0
3 and left to acclimate for 24 hrs. On Day 1, one of two treatments was assigned to each
4 experimental pool. For Treatment 1 (mixed-sex treatment, N=6) 5 male guppies
5 (23.1±0.2mm) were added to the pool with the 8 large females (34.0±0.4mm) and for
6 Treatment 2 (same-sex treatment, N=6), 5 small (male-sized) females (25.7±0.5mm)
7 were added to the pool with the 8 large females (34.0±0.3mm). The fish were left to
8 acclimatize for 24 hours, after which the social network structure of each population was
9 documented by recording shoal composition (photographed using a Nikon D40x digital
10 camera) once per minute for a 15 minute sampling period in each quarter of the pool by
11 an observer positioned at the side of the pool.

12

13 For each sampling event any two fish were defined as associating if they were observed
14 in the same shoal (defined as being within four body lengths of each other (see Croft et
15 al. 2004)). We used a Newman weighted association index (Newman 2001) to quantify
16 pair wise associations in which pairs of individuals observed in a group of size g are
17 given a weighting:

18

19
$$1/(g-1),$$

20

21 reflecting the fact that a given pair in a small group is more likely to be interacting than a
22 pair in a large group. These association weights were then accumulated over the sampling
23 period and the matrix of associations was used to construct social networks (Croft et al.

1 2008). For each replicate, the association matrix was used to construct two types of
2 networks: (1) a large-female social network (LFSN) that only included the large females
3 from a given pool and (2) an all-inclusive social network (AISN) that included all
4 individuals from a given pool. For each LFSN we calculated the average unweighted
5 degree measured as the average of the total number of network neighbours that each
6 female in the network had. We also calculated the average Newman association index for
7 each of these networks. For each AISN we calculated the average weighted degree of
8 classes of individuals (i.e. males and large females), measured as the average of the sum
9 of each individual's associations with others in the network (i.e. the edges linking each
10 individual to each of its network neighbours) (Wasserman & Faust 1994). Lower values
11 of weighted degree for an individual indicate lower levels of association for that
12 individual. For each AISN we also calculated the average weighted reach of classes of
13 individuals (again, males and large females). The weighted reach between a pair of
14 individuals is the value of the weakest connection along the strongest path (greatest sum
15 of ties) between those two individuals (Wasserman & Faust 1994) and indicates how
16 great the connectivity among individuals is with lower values indicating lower
17 connectivity. These two measures indicate how central a node is in the network and are
18 referred to as centrality measures (Wasserman & Faust 1994). Average degree, average
19 weighted degree and average reach were calculated in UCINET 6 for Windows (Analytic
20 Technologies, Inc).

21

22 We tested for differences in LFSN structure between treatments using a multivariate
23 general linear model with Newman association index and unweighted degree as

1 dependent variables. For the AISNs we combined the weighted reach and weighted
2 degree into a single measure of centrality using a principle component analysis and used
3 the first component for further analysis. We tested for treatment differences in large
4 female centrality with an independent samples t-test and for sex differences in centrality
5 in the mixed-sex networks with a paired t-test. All statistical tests were carried out in
6 SPSS 14.0 for Windows (SPSS, Inc.).

7

8 *The effect of males on female-female familiarity*

9

10 For the experiment testing the effect of males on the development of female-female social
11 recognition, pools were populated with fish (Day 0) in the same two sex ratios as in the
12 first experiment (8 large females (33.5 ± 0.2 mm) plus 5 males (25.1 ± 0.2 mm) and 8
13 large females (33.3 ± 0.2 mm) plus 5 small females (28.5 ± 0.2 mm)); this time with 12
14 replicates of each treatment (i.e. 24 networks total). In this experiment all fish in a
15 replicate were placed in the pools simultaneously on Day 0. Since we wanted to test for
16 social recognition among females, we had to control for the possible effect of habitat
17 odour cues that could be used to 'recognize' familiars during shoaling trials (see Ward et
18 al. 2005). Distinctive habitat odour cues were likely to develop in each of our semi-
19 natural pools and to control for this in our experimental design we subdivided each 180
20 cm diameter pool to give two semi-circular experimental pools. We used a mesh barrier
21 that restricted fish movement between pool halves and prevented the fish from the two
22 halves from having any tactile or visual contact. The water within each pool was
23 circulated daily to ensure adequate mixing of the halves. One replicate of a treatment was

1 then placed in one half with another replicate of the same treatment in the other half. In
2 this way the unfamiliar stimulus fish used during shoaling trials could come from the
3 same pool as the test fish, but without the test fish ever having encountered them.

4

5 Shoaling trials were run under natural light conditions on Days 4, 8 and 12. During trials
6 we measured the time that focal females spent with a shoal of two familiar females versus
7 a shoal of two unfamiliar females during a 10 minute test period. Fish were tested in a 40
8 x 20 cm tank containing water taken from their own pool. Shoal fish compartments (5 x
9 20 cm) were created by erecting a perforated acetate barrier at either end of the tank,
10 leaving a 30 x 20 cm open field between the shoal fish compartments as the test arena.
11 Focal fish were recorded as shoaling with stimulus fish if they were within 5 cm of the
12 barrier to shoal compartment. Two females from each replicate were tested singly on
13 each test day and their shoaling times averaged for further analysis so that only one value
14 for each replicate was included in the analysis per test day. Each female acted as a test
15 fish and as a stimulus shoal fish only once to avoid pseudoreplication.

16

17 We tested for the development of familiarity among large females using a repeated
18 measures general linear model (SPSS 14.0) as in Griffiths and Magurran (1997). We used
19 the proportion of time spent with each stimulus shoal as our dependent variable and
20 treatment and familiarity as the main effects with day as the within-subject effect.

21

22 ***Results***

23

1 *The effect of males on female social network structure*

2

3 We found striking differences between treatments in the network structure of the large-
4 female social networks ($F_{2,9}=23.975$, $p<0.0001$, Fig. 1a,b). There was a lower overall
5 level of association (fewer repeated interactions as indicated by a lower average Newman
6 association index) among females in the presence of males compared to when there were
7 no males present ($F_{1,10}=44.258$, $p<0.0001$, Fig. 1c) and large females had contact with
8 fewer other large females in the network (as indicated by a lower average unweighted
9 degree) when males were present compared to when they were not ($F_{1,10}=22.810$,
10 $p=0.001$, Fig. 1c).

11

12 In the analysis of the AISNs averages of weighted degree and weighted reach show that
13 large females in the same-sex social networks are more central in the network than large
14 females in mixed-sex social networks (t-test on PCA component 1: 95.3% of variance
15 with a 0.98 contribution of each variable, $t_{10}= -3.318$, $p=0.008$, Fig. 2a,b,c). They also
16 show that this is because males occupy the central positions in the mixed-sex networks
17 when compared to the large females in those networks (paired t-test on PCA component
18 1, $t_5=3.775$, $p=0.013$, Fig 2b,d).

19

20 *The effect of males on female-female familiarity*

21

22 We found a significant effect of the interaction between day, treatment and familiarity in
23 our repeated measures analysis ($F_{2,46}=4.270$, $p=0.021$) and the results of a post hoc

1 analysis of variance (Table 1) revealed that large females in the same-sex treatment
2 exhibited recognition of familiars on Day 8 and Day 12 while those from the mixed-sex
3 treatment did not (Fig. 3); although there was a tendency for these latter females to do so
4 on Day 12 with a slight negative preference (Fig. 3) that differed from the preference
5 exhibited by females in the same-sex treatment ($t_{21}=-2.796$, $p=0.011$).

6

7 *Discussion*

8

9 In this study we found that males greatly influenced female social structure, the ability of
10 females to develop social recognition and possibly even female-female association
11 preferences. In populations where females experienced sexual harassment they had a
12 lower degree of association with other females and were more peripheral in the social
13 network. Furthermore, females that were housed with males did not develop familiarity
14 with females from the same social network, although there was a tendency for them to do
15 so after 12 days with what appeared to be a preference for unfamiliar females. In contrast,
16 females that did not experience sexual harassment developed social recognition and
17 displayed a significant preference for others from within their own network after 8 days.
18 Overall our results suggest that male sexual harassment impacts social network structure
19 and has implications for the development of social recognition and female social bonds,
20 an effect that is likely to be relevant for a diverse array of taxa.

21

22 Across animal taxa individuals exhibit non-random social associations that ultimately
23 define the social structure of populations (Croft et al. 2008). Understanding why certain
24 patterns of association develop and how inter-individual associations and interactions

1 affect population level structure (e.g. connectedness and fragmentation) is essential in our
2 endeavour to unravel the functions and implications of social organization. The results of
3 our first experiment show that males have a previously unconsidered effect on female-
4 female social network structure, weakening female-female ties and leading to females
5 occupying more peripheral positions in the social network. Previous work on guppies has
6 shown that females may experience up to one forced copulation attempt (a sneaky
7 mating) from males every minute (Magurran & Seghers 1994b) and that this sexual
8 harassment constrains female behaviour leading to lost feeding opportunities (Magurran
9 & Seghers 1994a). The disruption of the female social structure most likely results from
10 males influencing female shoaling and foraging activities by harassing and chasing
11 individual females. Whilst disruption due to sexual harassment from males probably has
12 the largest effect on social network structure, females reducing their ties with other
13 females due to sexual interest in males could potentially be a factor in this equation. For
14 example, females may approach males to solicit mating events and thus reduce female-
15 female encounters. However, in the guppy system such events are rare in comparison to
16 the level of male coercion of females to obtain matings (Magurran & Seghers 1994b) and
17 sexual harassment is thus more likely to constrain female behaviour and determine social
18 structure.

19 .

20 Social associations in animals are often cultivated over time through repeated
21 interactions, which may be particularly important for the development of social
22 recognition (Ligout & Porter 2006). Previous work on guppies suggests that social
23 familiarity may take an extended time period to develop, up to 12 days (Griffiths &

1 Magurran 1997). However, more recent work on three-spined sticklebacks (*Gasterosteus*
2 *aculeatus*), suggests that social recognition can be achieved quickly when habitat odour
3 differs between familiar and unfamiliar fish (Ward et al. 2005). Our experimental setup
4 allowed us to control for the effect of habitat mediated familiarity and shows that the
5 development of social familiarity between females is disrupted by the presence of males,
6 presumably due to the observed limited contact between females. The hindrance of the
7 development of inter-individual familiarity is likely to have fitness consequences
8 (Griffiths & Ward 2006; Ligout & Porter 2006; Silk 2007a). For example, previous work
9 with fish has shown that shoals of familiar individuals out-perform randomly assembled
10 shoals in foraging tasks (Morrell et al. 2008) and display more co-ordinated antipredator
11 behaviour, which is thought to lead to a reduced risk of predation (Chivers et al. 1995).
12 Social familiarity is also known to be important for mediating aggression (Utne-Palm &
13 Hart 2000) and stabilizing group hierarchy (Höjesjö et al. 1998). Thus one may
14 hypothesise that female groups with reduced social familiarity due to male harassment
15 may suffer decreased foraging success, increased predation risk and increased aggression.
16
17 Although marginally non-significant, our results also suggest that females that experience
18 male harassment may indeed develop social recognition, but it undoubtedly takes them
19 longer to do so. Furthermore, whilst we observe positive preference for familiar
20 individuals between females in the absence of male harassment, females that experienced
21 sexual harassment actually preferentially associated with unfamiliar individuals once
22 familiarity started to develop. Social preferences for familiar individuals in fish and other
23 taxa are well documented (see Griffiths & Ward 2006; Ligout & Porter 2006 for reviews

1 in fish and mammals). However, a preference for associating with unfamiliar individuals
2 has been reported in at least one study, where it appeared to be linked with unfavourable
3 environmental conditions (Frommen et al. 2007). It is possible that the observed tendency
4 for a preference for unfamiliar individuals in our study is also a response to unfavourable
5 conditions, that is, high levels of male harassment perhaps leading to decreased foraging
6 success. Preferring to associate with unfamiliar individuals may be a way for individuals
7 to change their social environment in an attempt to ensure more favourable conditions.
8 The role of the social and ecological environment in driving preference for unfamiliar
9 versus familiar individuals certainly makes for an interesting avenue for future research.

10

11 A female's fitness is influenced by many ecological factors. The results presented here
12 provide the first insight into the effect of male sexual harassment on the disruption of
13 female social networks and social recognition, which we predict will have fitness
14 consequences and represent a key currency in the trade-off between potentially costly
15 male avoidance behaviour and acceptance of male sexual advances. Our work leads us to
16 hypothesise that in wild populations where females experience sexual harassment, social
17 network structure and social recognition will differ as a function of male density and the
18 opportunity for females to avoid sexual harassment. Future studies testing these
19 predictions in wild populations are eagerly anticipated. In conclusion, in a recent paper
20 Rankin and Kokko (2007) ask "do males matter?" in the context of population dynamics,
21 from our results, we think that we can answer this very simply: "yes, they do".

22

1 **Acknowledgements:** We thank Mathew Edenbrow for assistance in the field and S.
2 Alonzo and two anonymous referees for insightful comments on a previous version of the
3 manuscript. Funding was provided to DPC by NERC (NE/E001181/1).

4

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Treatment	Day	<i>F</i> _{1,22}	<i>P</i>
Male-female	4	0.115	0.738
	8	0.024	0.878
	12	2.900	0.103
Female-Female	4	0.684	0.417
	8	11.500	0.003
	12	18.200	<0.0001

3

4 **Table 1.** Results of post-hoc analyses of variance with familiarity as the main effect to
5 test the interaction Day*Treatment*Familiarity in the repeated measures general linear
6 model (see text).

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1 **Figure 1.** (a) Example of large-female social networks observed in the mixed-sex
2 treatment and (b) in the same-sex treatment. Edges are weighted by the Newman
3 association scores (0.2 to 8) and can be compared across the two graphs. (c-d) Summary
4 of network measures on female-female associations illustrating the average Newman
5 index (c) and the average unweighted degree (d) for large-female social networks in the
6 two treatments. Error bars represent standard error.

7

8 **Figure 2.** (a) Example of all-inclusive social networks observed in the mixed-sex
9 treatment (large females (●); males (○)) and (b) in the same-sex treatment (large females
10 (●); small females (○)). Edges are weighted by the Newman association scores (0.2 to 8)
11 and can be compared across the two graphs. (c-f) Summary of network measures on
12 associations illustrating the average weighted degree (c) and the average weighted reach
13 (d) for all-inclusive social networks in the two treatments and the average weighted
14 degree (e) and the average weighted reach (f) for males and females in all-inclusive social
15 networks in the mixed-sex treatment. Error bars represent standard error.

16

17 **Figure 3.** Differences in the proportion of time focal fish spent with familiar fish and
18 unfamiliar fish of the total time they spent shoaling (familiar minus unfamiliar) (same-sex
19 treatment (○), mixed-sex treatment (●)). Positive values indicate a bias for shoaling with
20 familiar individuals. Error bars represent standard error.

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