

1 **Do you like me as much as I like you? Equitability in guppies' social association**

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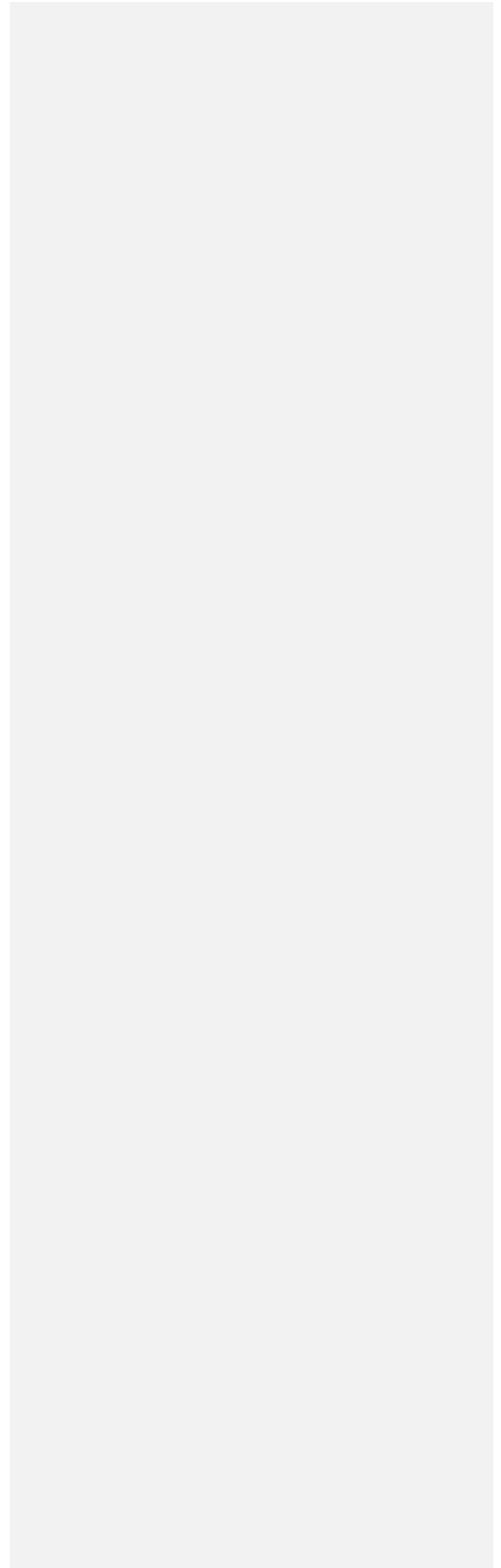
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8 **Abstract**

9 Growing evidence indicates that at least some aspects of the human social system find parallels in  
10 non-human primates and other taxa in which individuals form enduring, equitable and highly  
11 differentiated social relationships, often referred to as 'friendships'. Several fish species are  
12 characterized by social systems in which individuals show preference to interact with specific  
13 group mates. However, there is no clear evidence that such relationships are equitable. We  
14 addressed this issue in the guppy (*Poecilia reticulata*), a species in which social network analysis  
15 has evidenced non-random social associations between individuals in the shoal. To assess the  
16 equitability of the social associations we estimated the reciprocal preference of two familiar  
17 guppies over unfamiliar individuals; familiarity was developed in groups of either two or six  
18 individuals. Irrespective of the group size during familiarization (2 or 6 individuals) we found a  
19 significant among-pairs variation and a positive within-pair correlation in the preference for the  
20 familiar fish, indicating that social associations are equitable in this species. In a second  
21 experiment, we showed that these social associations require previous familiarization between  
22 individuals to develop and are not based on spontaneous preferences or passive assortments. Our  
23 results demonstrate that familiar guppies develop equitable social associations. Guppies and other  
24 social fish might provide a valuable system to test the hypotheses about the evolution of  
25 vertebrate sociality.

26

27

28 **Keywords:** equitability, familiarity, *Poecilia reticulata*, social preference, social associations.

## 29 Introduction

30 One of the key features of human sociality is that the strength of the social relationships between  
31 pairs of familiar individuals is variable and usually equitable [1, 2]. At one extreme of a continuum,  
32 some individuals develop strong, durable and equitable social bonds, often referred to as  
33 friendships; at the opposite extreme, other individuals avoid each other. Also non-human primates  
34 that form stable social groups are characterized by social bonds qualitatively similar to human  
35 friendship (e.g. [3-6]). For example, female baboons (*Papio spp.*) are involved both in a broad  
36 network of weak relationships and few strong dyadic social bonds [7, 8]. Similarly, in chimpanzees  
37 (*Pan troglodytes*) and in a macaque species (*Macaca assamensis*), some individuals in the same  
38 group rarely interact, while others form stable and enduring social bonds [4, 9]. Despite being a  
39 relevant feature of human friendship [10, 11], equitability has been investigated and reported in  
40 other primates only in the last decade [7, 12, 13]. Equally reciprocated grooming (i.e. a form of  
41 affiliative body contact) is commonly used as a proxy of equitability: the more grooming an  
42 individual provides to a partner the more it receives from the same individual in return [12, 13]. In  
43 non-human primates, these social bonds have been demonstrated to provide fitness advantages  
44 [8, 14, 15] suggesting that they might be maintained by selection.

45 Although animal friendship has been largely studied in primates, social relationships with similar  
46 characteristics may occur also in other mammals, such as lions, dolphins, sea lions, feral horses  
47 and kangaroos (e.g. [16-20]), and in some social birds (e.g. [21-23]) and fish (e.g. [24-26]). Given  
48 the absence of grooming behaviour, studies on these species typically exploit other measures to  
49 quantify social relationships [27]; among these measures, the most common is 'proximity' (e.g.  
50 [28-30]; reviewed by [31, 32]). Social association between two individuals can be identified  
51 because of their high spatial proximity [27], operatively defined as high amount of time spent near  
52 each other (e.g. [33]).

53 Concerning fish, some species show very different social systems compared to complex primate  
54 societies, yet there is evidence of clearly differentiated social relationships between individuals.  
55 For instance, the guppy, *Poecilia reticulata*, forms small shoals (usually from 2 to 20 individuals)  
56 characterized by individuals continuously moving among shoals and high fission-fusion dynamics;  
57 further, individuals disperse overnight, resulting in the breakdown of shoal composition and a  
58 reassembly every morning [34]. However, social network analyses have revealed that some  
59 individuals, especially females, consistently prefer to interact with specific shoal mates [24, 35,  
60 36], suggesting differences in the strength of within-shoal associations.

61 These associations observed in fish may reflect similar social relationships (i.e. friendship) as those  
62 observed in other taxa [1, 2, 31], or may be determined by other processes that do not require the  
63 development of equitable dyadic social bonds. In several fishes, including guppies, individuals  
64 show a social preference for familiar individuals (e.g. [37-42]) or may associate preferentially with  
65 individuals that have experienced the same diet or habitat conditions as themselves [43, 44].  
66 Given that the composition of the social groups in fish is usually less stable than in primates due to  
67 movements of individuals between groups over short time frames [34], individuals with different  
68 levels of familiarity and similar experiences often coexist in the same group. This might account for  
69 the association patterns observed in social networks. More importantly, it is not clear whether  
70 dyadic associations are equitable in fish.

71 The aim of this study was to assess whether fish can develop equitable within shoal social  
72 associations when the degree of familiarity is controlled for. Firstly, we estimated equitability of  
73 social associations in guppies that previously familiarized for an equal period of time by measuring  
74 their reciprocal preference compared to that for unfamiliar individuals. If guppies' social  
75 associations resulted equitable in spite of the controlled time of familiarization, we expected to  
76 find a positive correlation between the social preferences of each fish towards the other familiar

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84 fish. We tested our hypothesis in two different conditions: half of the subjects familiarized in pair,  
85 whereas the other half familiarized in groups formed by six individuals. Since differentiated and  
86 equitable preference between individuals may result from assortment based on phenotype  
87 similarity [45], we performed a further condition as above but using randomly chosen pairs of  
88 unfamiliar individuals (unfamiliar condition), thereby excluding familiarity. We expected that the  
89 phenotypic assortment alone, without the previous familiarization between the individuals, does  
90 not suffice to develop equitable social relationships.

91

## 92 **Methods**

### 93 Experimental fish

94 Fish used in this study were descendants of wild-caught guppies from the Tacarigua river in  
95 Trinidad. Guppies were maintained in large stock tanks (ca. 100 individuals/tank; ca. 1:1 sex-ratio)  
96 and were free to interact and mate. Temperature was kept nearly constant at  $26 \pm 1$  °C and  
97 illumination set on a 12h:12h light/dark cycle. Fish were fed with both live *Artemia salina* nauplii  
98 and commercial food (DuplarinS) twice per day. Experimental fish were randomly chosen from  
99 twelve stock tanks and allocated to a group or pair in order to avoid prior familiarity. Fish from the  
100 same stock tank were allocated to different groups or pairs because in this species fish recognize  
101 familiar individuals after prolonged periods of isolation [46]. In the six-individual familiarization  
102 condition, we formed 20 groups consisting in 6 initially unfamiliar females (120 females overall); in  
103 the two-individual familiarization condition, we formed 20 pairs in which females were initially  
104 unfamiliar (40 females overall) (see Fig. 1). The females in a group or in a pairs were collected from  
105 different stock tanks to ensure that they were unfamiliar before the beginning of the experiment.

106 In the unfamiliar condition, we used 60 unfamiliar females (see Fig. 1). At the end of the  
107 experiment, we measured body size (see below for further details) and then fish were released in

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115 post-experimental tanks.

116 *Familiarization procedure*

117 The six-individual groups familiarized in 8-L tanks (1.4 L/fish) whereas the two-individual groups  
118 familiarized in 3.5-L tanks (1.75 L/fish) (see Fig. 1). The familiarization lasted 12 days for both  
119 conditions, a duration sufficient for the development of familiarity in this species [38]. All the  
120 familiarization tanks were placed in a Tecniplast ZebraTank system, which allowed the  
121 maintenance of standard condition of pH, temperature and light, and were enriched with java  
122 moss (*Taxiphyllum barbieri*). During familiarization, fish were fed as described for maintenance. In  
123 the control condition fish did not undergo familiarization before the binary preference test and  
124 thus, we individually isolated 60 females in 2-L tanks.

125 *Binary preference test*

126 At the end of the familiarization, we performed a binary preference test based on a well-  
127 established procedure [43, 47, 48]. The experimental tank was a glass aquarium (48 x 20 cm, 30  
128 cm high, and filled with 16 cm of well water) provided with natural gravel and divided into three  
129 sectors by two transparent plastic partitions. The central, larger sector (24 x 20 cm) housed the  
130 focal fish during the experiment, while the lateral sectors (12 x 20 cm each) housed the familiar  
131 and unfamiliar stimuli, respectively. The partitions were provided with holes, allowing the focal  
132 fish to perceive the olfactory cues of the stimuli. Two 15-W fluorescent lamps illuminated the  
133 lateral sectors, whereas the central sector received indirect light from the lateral sectors. Light in  
134 the room was switched off allowing the observation the fish without being seen. We recorded the  
135 time spent by the focal fish near the familiar individual versus an unfamiliar individual [48], i.e.  
136 spatial proximity, as measure of social associations [27, 49]. In the two-individual condition, we  
137 tested both individuals whereas in the six-individual condition, we tested two randomly-chosen  
138 individuals *per* group (Fig. 1). As unfamiliar stimuli we used a fish of another group from the same

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142 familiarization condition. Thus, each experimental fish was tested as focal fish, as familiar stimulus  
143 and as unfamiliar stimulus in a randomized order. One hour before the beginning of the test the  
144 familiar and the unfamiliar stimuli were introduced into the lateral sector of the experimental  
145 tank. The left/right location of the familiar stimulus was alternated between trials to avoid bias.  
146 The focal fish was introduced into the central sector 2 min before the start of the experiment for  
147 habituation. Two marks on the bottom of the tank 6 cm away from each transparent partition  
148 virtually divided the central sector in three areas: a central no-choice area, a choice area for the  
149 familiar stimulus and a choice area for the unfamiliar stimulus (see Fig. 1). Following previous  
150 studies [50, 51], we recorded the position of the subject across these three areas every 12 s for 10  
151 min. The recording was performed by an observer sitting motionless beside the tank and behind a  
152 curtain. In the control condition, after 24 h from isolation, we randomly assigned 20 females as  
153 focal fish. Each focal individual was tested in a binary preference test in which the subject could  
154 choose between two unfamiliar conspecifics matched for size (Fig. 1). After this trial, we randomly  
155 chose one of the two unfamiliar stimuli as focal fish for the second trial. The second trial was  
156 performed 24 h after the first trial and the focal fish could choose between an unfamiliar stimulus  
157 and the fish that was the focal in the first trial (Fig. 1). Other details were identical to those  
158 described above.

### 159 *Body size measurements*

160 In some contexts, size might affect social preference of fish [25, 52]. To avoid this confound, we  
161 matched as much as possible the size of the fish in each group and in the same binary preference  
162 test. This size matching was done by visually comparing the size of the fish before the  
163 familiarization to avoid disturbance. At the end of the experiment, we performed a more accurate  
164 estimation of females' body size in order to statistically test the effect of body size on social  
165 preference. Each fish tested was placed in a small glass tank (20 x 10 x 2 cm) and was held to the

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**Deleted:** In this experiment fish did not undergo familiarization before the binary preference test. We randomly chose 60 females from the stock tanks and then we individually isolated the females in 2-L tanks. A...

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**Deleted:** To test whether our subjects developed familiarity during the familiarization period, we performed a binary preference test for the familiar group [38]. One day after the completion of the previous tests, the two focal fish of each six-individual group were observed in the choice between the familiar group and an unfamiliar group. Outside the use of stimulus shoals instead of individuals, other details of the procedure were identical to those described above. ¶

184 glass with a flat plastic net. The fish was then digitally photographed on its left side along with a  
185 scale for calibration using a Canon 450D. We used a software for image analysis (ImageJ:  
186 <http://rsbweb.nih.gov/ij/download.html>) to measure the distance between the snout and the  
187 base of the tail (standard length, SL), the total length (TL) and the total area of the body (body  
188 area, BA) from the digital images.

189  
190 **Statistical analysis**  
191 Social preference for the familiar stimulus was calculated as the time in which the focal fish was  
192 observed within 6 cm from the sector with the familiar stimulus over the total time spent in the  
193 two choice areas [53, 54]. **Firstly, we tested for equitability in the social preference of the two**  
194 **individuals in the pair running a Pearson's correlation analysis for each condition. Comparisons**  
195 **between the correlation coefficients were done using Fisher's r to z transformation [55]. After**  
196 **that, we performed also a repeatability analysis in the social preference of the two individuals in**  
197 **the pair to estimate the standard error (SE) associated to the repeatability coefficient (R). R was**  
198 **estimated following Lessells and Boag [56] and SE according to Becker [57].**  
199 **Then, we tested** whether preference for the familiar companion differed between familiarization  
200 conditions, **running a** mixed-effect ANOVA, in which social preference for the familiar stimulus was  
201 fitted as dependent variable, familiarization condition was included as fixed effect and pair  
202 identity as random effect. Before the analysis, we controlled for homogeneity of variance  
203 (Levene's test) in social preference between the familiarization conditions.  
204 **Finally, we** calculated an index adapted from primate research [e.g. 7, 12, 13] to describe  
205 equitability of guppies' social associations (hereafter 'ESA score'). ESA score was calculated as  $1 -$   
206  $[(TF_A - TF_B) / (TF_A + TF_B)]$  where TF was the time spent with the familiar companion by each

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**Moved up [1]:** In this experiment fish did not undergo familiarization before the binary preference test. We randomly chose 60 females from the stock tanks and then we individually isolated the females in 2-L tanks. After 24 h, we randomly assigned 20 females as focal fish. Each focal individual was tested in a binary preference test in which the subject could choose between two unfamiliar conspecifics matched for size. After this trial, we randomly chose one of the two unfamiliar stimuli as focal fish for the second trial. The second trial was performed 24 h after the first trial and the focal fish could choose between an unfamiliar stimulus and the fish that was the focal in the first trial. Other details were identical to those of described for experiment 1. ¶

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**Deleted:** Then, we tested for equitability running a Pearson's correlation analysis for each familiarization condition to correlate the social preference of the two individuals in the pair. Comparisons between the correlation coefficients were done using Fisher's r to z transformation [55]. For each familiarization condition, we also performed a repeatability analysis in the social preference of the two individuals in the pair. We calculated the repeatability coefficient (R) estimated following Lessells and Boag [56] and the associated standard error (SE) to R was estimated according to Becker [57]. Then, we ran a mixed-effects ANOVA on the fish from the six-individual familiarization condition to compare the time spent near the familiar and the unfamiliar shoal. Model included stimulus type (familiar and unfamiliar stimulus) as fixed effect and, pair identity and female identity as a random effect to account for the non-independence of data. ...

**Moved up [2]:** we tested for equitability running a Pearson's correlation analysis for each familiarization

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278 individual in the pair (individual A and individual B). The ESA scores ranges between 0 and 1 and an  
279 ESA value of 1 indicates a perfect reciprocity between the time spent by each individual with the  
280 familiar companion. We performed an ANOVA and a post hoc analysis to compare the ESA scores  
281 among conditions.

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282 Body size measurements were highly correlated, showing correlation coefficients (r) ranging from  
283 0.938 to 0.965 ( $p < 0.001$ ), thus only body area was considered in the further analyses (other body  
284 size measures provided similar results). We ran a Pearson's correlation analysis for each condition  
285 between the standardized difference in body area of females in the same pair and the ESA score of  
286 the pair. We did not find a significant correlation between ESA score and the difference in body  
287 area of the two fish (six individuals:  $r = 0.026$ ,  $p = 0.915$ ,  $N = 20$ ; two individuals:  $r = 0.043$ ,  $p = 0.856$ ,  
288  $N = 20$ , unfamiliar individuals:  $r = 0.217$ ,  $p = 0.357$ ,  $N = 20$ ).

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289 Statistical analyses were performed using SPSS (v21.0) and R (v1.1.423) statistical software.

Deleted: ). Also in experiment 2, ESA score of each pair did not significantly correlate with the standardized difference in body area of females in the same pair (unfamiliar individuals:

## 291 Results

292 Both in the two- and six-individual familiarization condition, the preference for the familiar  
293 stimulus expressed by two fish from the same familiarization group was positively correlated  
294 (Pearson's correlation: two individuals:  $r = 0.556$ ,  $p = 0.011$ ,  $N = 20$ ; six individuals:  $r = 0.642$ ,  $p = 0.002$ ,  
295  $N = 20$ , Fig. 2), indicating that social relationships were significantly equitable. The strength of the  
296 correlation between the reciprocal preference of the two familiar fish did not significantly differ  
297 between the two familiarization conditions ( $z = 0.39$ ,  $p = 0.697$ ). When two unfamiliar individuals  
298 were paired randomly, their reciprocal social preferences were not significantly correlated  
299 (Pearson's correlation:  $r = 0.192$ ,  $p = 0.417$ ,  $N = 20$ ). Repeatability analysis confirmed that social  
300 preference of the two individuals were significantly repeatable in both the familiarization  
301 conditions (two individuals:  $R \pm SE = 0.390 \pm 0.194$ ; six individuals:  $R \pm SE = 0.598 \pm 0.147$ ), but not

Deleted: Experiment 1  
Mean social preference for the familiar companion was not significantly different between the two familiarization conditions (familiarization condition:  $F_{1,38} = 0.066$ ,  $p = 0.799$ ) but we found a significant effect of pair identity in social preference among familiar pairs (pair identity:  $F_{1,38} = 3.098$ ,  $p < 0.001$ ), suggesting that variability in social preference was lower within pairs than between pairs. Pair identity was also significant when performing separate analyses for each familiarization condition (two individuals:  $F_{1,19} = 2.280$ ,  $p = 0.037$ ; six individuals:  $F_{1,19} = 3.976$ ,  $p = 0.002$ )....

321 between unfamiliar individuals ( $R \pm SE = 0.208 \pm 0.219$ ). These results suggest that previous

322 familiarization is needed to observe reciprocated social association between individuals.

323 Mean social preference for the familiar companion was not significantly different between the

324 two familiarization conditions (familiarization condition:  $F_{1,38} = 0.066, p = 0.799$ ) but we found a

325 significant effect of pair identity in social preference among familiar pairs (pair identity:

326  $F_{1,38} = 3.098, p < 0.001$ ), suggesting that variability in social preference was lower within pairs than

327 between pairs. Pair identity was also significant when performing separate analyses for each

328 familiarization condition (two individuals:  $F_{1,19} = 2.280, p = 0.037$ ; six individuals:  $F_{1,19} = 3.976,$

329  $p = 0.002$ ). On the contrary, when fish were unfamiliar, variability in social preference was not

330 significantly lower within pairs than between pairs ( $F_{1,19} = 1.526, p = 0.178$ ).

331 The distribution of ESA scores provides a measure of how the characteristics of social relationships

332 were distributed between the familiar conditions. ESA scores were left-skewed in both

333 familiarization conditions (two individuals: skewness = -1.379,  $z = 3.400, p = 0.001$ ; six individuals:

334 skewness = -0.722,  $z = 1.979, p = 0.048$ ; Fig. 4) with most of the values above 0.5, which indicates

335 highly equitable social relationships. In particular, when females familiarized in two-individual

336 groups, all the pairs formed highly equitable social associations; when females familiarized in six-

337 individual groups, 90% of pairs formed highly equitable social associations (Fig. 4). When females

338 were unfamiliar ESA scores were not significantly left-skewed (unfamiliar individuals: skewness = -

339 0.473,  $z = -1.041, p = 0.298$ ). A one-way ANOVA showed a significant main effect of condition on ESA

340 scores ( $F_{2,59} = 6.2751, p = 0.003$ ), and post hoc analysis revealed significant difference in ESA scores

341 between familiar and unfamiliar individuals (six-individual familiarization condition — unfamiliar

342 condition:  $p = 0.006$ ; two-individual familiarization condition — unfamiliar condition:  $p = 0.007$ ).

343 **Discussion**

**Deleted:** . When we measured the preference for the familiar group, we found that guppies spent significantly more time close to the familiar versus the unfamiliar shoal (mean  $\pm$  SD =  $0.66 \pm 0.19$ ;  $F_{1,78} = 46.324$ ;  $p < 0.001$ ). ¶

¶ Experiment 2 ¶  
When two unfamiliar individuals were paired randomly, their reciprocal social preferences were not significantly correlated (Pearson's correlation:  $r = 0.192, p = 0.417, N = 20$ ) and variability in social preference did not differ among pairs ( $F_{1,19} = 1.526, p = 0.178$ ). Repeatability analysis confirmed that social preference of the two individuals in the pair were not significantly repeatable ( $R \pm SE = 0.208 \pm 0.219$ ). Th

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**Deleted:** ESA score<sup>+</sup>  
The ESA scores did not significantly differ with respect of group size during familiarization suggesting that social relationships are equally differentiated in groups of 2 and 6 familiar individuals (ESA:  $t_{1,38} = 0.060, p = 0.952$ ). ...

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**Deleted:** When females were unfamiliar ESA scores were not significantly left-skewed (unfamiliar individuals: skewness = -0.473,  $z = -1.041, p = 0.298$ ) and did not significantly differ with respect of familiarity suggesting that social associations differed in equitability between familiar and unfamiliar individuals (ESA:  $t_{1,23} = 2.705, p = 0.013$ ). ¶

376 In non-human primates, individuals develop social relationships that are equitable, similarly to  
377 what is observed in human friendship [7, 12, 13]. Outside primates, many mammals [58] and some  
378 social birds [59] have received increased interest in the last decade, and friendships have been  
379 reported in a diversity of taxa [2, 58, 59]. Also in some social species of fish, individuals  
380 consistently associate over time with specific individuals [25, 60, 61]. Although social fish species  
381 are often subjected to rapid fission-fusion dynamics, the persistence of within-shoal social  
382 associations over time suggests that also fish may engage in equitable social relationships as  
383 observed in other taxa. The results of our study on guppies support this hypothesis.

384 In our ~~experiment~~, fish previously familiarized either in two-individual or six-individual groups and  
385 showed a significant within-pair consistency in the preference for the familiar individual: in some  
386 pairs, both individuals showed a high preference for the familiar fish, whereas in others pairs  
387 familiar individuals tended to avoid each other. As a consequence, the strength of the preference  
388 for the familiar fish was positively correlated between the two fish in the pair. This suggests that  
389 most of social associations due to familiarity were equitable irrespective of their strength, as  
390 confirmed also by the skewness of ESA values.

391 The analysis of social networks has previously demonstrated that social preferences between  
392 individuals within a shoal are variable in guppies and other fish species: there are pairs of  
393 individuals that tend to interact more often [24, 26, 35, 36]. However, the nature of such  
394 interactions was not fully explored. For example, two fish in a shoal may interact more frequently  
395 because they are more familiar to each other, or because they have similar habitat preferences,  
396 movement speed or foraging behaviour and hence they spent more time together (i.e. passive  
397 assortments) [45, 62]. In our ~~experiment~~, all the fish experienced the same level of familiarity, as  
398 they were kept together for the same time, and we can therefore exclude differences in familiarity  
399 (e.g. [38]) as an explanation for the observed equitability in social preferences. The observed

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403 pattern of association, however, may also reflect assortment based on phenotype matching [25,  
404 43, 44, 63]. One trait that has been extensively shown to influence assortment among fish is body  
405 size [25, 52] **but we** found that body size matching was not correlated with the strength of the  
406 reciprocal social preference. To assess whether other morphological or behavioural traits drive the  
407 observed reciprocal social preference [62], we tested whether unfamiliar individuals show the  
408 same pattern of social preference observed **when fish familiarized**. We found that, when fish were  
409 unfamiliar, female guppies did not show equitable social preferences. During the test with  
410 unfamiliar conspecifics, the focal fish could base its choice only on the morphological traits of the  
411 stimulus fish and on some behavioural characteristics, such the swimming behaviour, and the  
412 chemical signals. Our results suggest that these factors alone were not sufficient to generate  
413 equitable social preferences and it is probably required a more prolonged interaction between  
414 individuals, as it occurs during familiarization. Altogether, our results indicate that familiarization  
415 is necessary for developing equitable social associations similar to what observed in experiment 1  
416 and that the association patterns that we observed might not be simply explained by spontaneous  
417 choices based on phenotype/behavioural matching.

418 In primates and other mammals, there are many factors that potentially contribute to generate  
419 social relationships between individuals: relatedness [18, 64], age [64, 65], and social status [13,  
420 66] largely predict social association patterns. In guppies, it has been recently demonstrated that  
421 exposure to high perceived risk of predation increases the emergence of relationships between  
422 females [36] and these relationships seem to be important in driving exploration of a novel  
423 foraging task [67]. Hence, predation risk might be a factor favouring equitable sociable  
424 relationships in guppies. The role of other factors remains to be addressed. For example, some  
425 other extrinsic factors such as food availability, parasitic load, density and sex ratio might affect  
426 social differentiation within fish group [45, 62]. Intrinsic characteristics of the individual fish may

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431 also generate assortative interactions, such as personality, previous experience and cognitive skills  
432 [68-71]. For instance, Croft and colleagues [72] showed that in a social network individuals were  
433 assorted by behavioural traits (i.e. predator inspection and shoaling tendency). Moreover, shy fish  
434 had more social connections than bold fish and these were on average stronger. Also other studies  
435 on social networks evidence that individuals with many connections are connected with  
436 individuals that have also many connections [e.g. 36, 73]. Guppies show a large individual variation  
437 in sociability: some individuals appear to consistently interact with other individuals, move in  
438 group, and actively seek the proximity of other conspecifics; others appear less motivated to join  
439 groups, often explore novel environments and disperse further from the original group [48, 68,  
440 74]. Accordingly, one explanation of our results may be that highly sociable individuals tend to  
441 prefer each other and aggregate together more frequently, while others tend to be less sociable  
442 avoiding relationships with other individuals and are also avoided by sociable individuals [73].

443 Among fish species there is at least one example of equitable behaviour: guppies and sticklebacks  
444 (*Gasterosteus aculeatus*) exposed to a potential predator perform a typical inspection behaviour.  
445 In a series of studies it has been show that individuals of these species show an association  
446 preference for those individuals that cooperate during predator inspection [75-77]. This behaviour  
447 can be associated to some form of equitability, though very different from the one of this study. It  
448 is however possible that previous social associations are required for cooperative behaviours to  
449 develop. All in all, these data might be considered evidence that equitability and reciprocation  
450 might be a common feature of fish behaviour.

451 Equitable social relationships in primates have been often associated with fitness benefits. For  
452 example, in female chacma baboons (*Papio ursinus*) infant survival to one year and infant  
453 longevity are predicted by the number of a female's weak social relationships but not by the  
454 number of her strong social relationships ([8], but see [6]). In contrast, females who form stronger

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456 and more stable social relationships with other females live significantly longer than females who  
457 form weaker and less stable relationships [3]. It remains to be addressed whether differentiated  
458 and equitable social bonds confer fitness advantages also in fish shoals that are often  
459 characterized by high occurrence of fission-fusion events.

460 Another result of our study is that equitable social associations can develop during familiarization  
461 independently of group size, at least for cases tested here (2 or 6 individuals). It has been recently  
462 proposed that the strength of social relationships might negatively depend on group size in fish  
463 [36], though it is not known whether this effect is due to cognitive constraints limiting individual  
464 recognition and therefore the degree of familiarization in large groups [78]. Our result suggests,  
465 instead, that equitable strong and weak social relationships develop irrespective of group-size  
466 familiarization conditions. It will be interesting to test if and at which group size the equitability  
467 will start to decrease. If equitable social relationships are associated with substantial fitness  
468 benefits, it may be predicted that average size of female guppy shoals does not exceed this value.

469 In conclusion, our findings align with the evidence found in mammals and birds [1, 31] and suggest  
470 that the development of equitable social associations may be a phenomenon more widespread  
471 than previously thought. The similarity between the social relationships observed in such distantly  
472 related groups, at least for some aspects, might reflect similar selective pressures and convergent  
473 evolution (but see [27]). There are many questions on sociality arising from studies on non-human  
474 primates for which there is not a clear answer. For example, it is not known how social  
475 relationships affect the dynamic of the entire group or which extrinsic and intrinsic factors  
476 determine the type of social interactions between individuals. Contrary to primates and other  
477 mammals, fish are simple to handle and to experimentally manipulate and might provide an  
478 important contribution for answering these general questions on the evolution of sociality.

479

480 **Ethics**

481 This research followed the Animal Behaviour Society Guidelines for the Use of Animals in Research  
482 and was approved by Ethical Committee of the University of Padova (protocol number: 68/2016 to  
483 SC). Fish used were descendants of wild-caught fish, so no transport of the experimental fish was  
484 necessary. Our behavioural tests did not involve any invasive manipulations and after the study, all  
485 fish were returned to stock tanks.

486 **Competing Interests**

487 The authors declare no competing interests.

488 **Funding**

489 The experiments were supported by grants from the University of Padova to MG (grant no. PRAT  
490 2015 CPDA153859) and to AP (grant no. 632 CPDA120105/12 and 60A06-7955/12). SC and TLX  
491 were supported by a fellowship from the University of Padova (SC: grant no. PRAT 2015  
492 CPDA153859; TLX: grant.no PRAT 2014 CPDA131092/13).

493 **Acknowledgements**

494 We thank the Botanical Garden of the University of Padova, and Laura Cioetto and Cecilia

495 Melarancio for help with fish husbandry. We also thank Julie Duboscq [for commenting on a](#)  
496 [previous version of the manuscript.](#)

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**Deleted:** and an anonymous referee for their helpful suggestions.

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698  
699 **Figure legends**

700 ~~Figure 1: Three dimensional view of the experimental apparatus: the focal individual is placed in~~  
701 ~~the central compartment in both visual and olfactory contact with the familiar and the unfamiliar~~  
702 ~~stimulus placed in the lateral compartments.~~

703  
704 Figure 2: Correlations between the social preference for the familiar individual of the two  
705 individuals (individual A and B) in each pair as a function of familiarization condition. Solid lines  
706 and solid circles referred to six-individual familiarization condition ( $r=0.642$ ,  $p=0.002$ ), while  
707 dashed lines and open circles referred to two-individual familiarization condition ( $r=0.556$ ,  
708  $p=0.011$ ) **+ unfamiliar**.

709  
710 Figure 3: Social preference (solid square) for each individual (A and B) of the pair and the  
711 associated 95% confidence intervals (following Jeffreys method). Histograms represents the  
712 binomial total.

713 Figure 4: Histograms showing a) the distribution of the strength of social relationships (SSR)  
714 relative to the six-individual familiarization condition (left panel) and the two-individual  
715 familiarization condition (right panel) and b) the distribution of the equitability of social  
716 relationships (ESR) relative to the six-individual familiarization condition (left panel) and the two-  
717 individual familiarization condition (right panel).