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1 **Submissive behaviour is mediated by sex, social status, relative body size and shelter**
2 **availability in a social fish**

3

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20

21 Acting submissively may inhibit aggression and facilitate the termination of contests without

22 further escalation. The need to minimize conflict is vital in highly social species where within-

23 group interactions are frequent, and aggression can dampen group productivity. Within social

24 groups, individual group members may modulate their use of submissive signals depending on
25 their phenotype, the value of the contested resource, their relationship to the receiver of the
26 signal and the characteristics of the local environment. We predicted that submissive behaviour
27 would be more common when signallers had limited ability to flee from conflict, when signallers
28 were of a low rank within the group, when signallers and receivers differed substantially in body
29 size (and thus in fighting ability), and when signallers and receivers were of opposite sex and
30 therefore not directly in competition over reproductive opportunities. We tested these predictions
31 using social network analyses on detailed behavioural observations from 27 social groups of the
32 cooperatively breeding cichlid fish *Neolamprologus pulcher*. Congruent with our prediction,
33 submissive behaviour was more common when there were fewer shelters available, suggesting
34 that constraints on fleeing behaviour may increase the use of submission. Also fitting with
35 predictions, submissive behaviour was more common with increasing body size asymmetry
36 between the competitors, among lower ranked fish and in interactions between opposite-sex
37 dyads, which supports the idea that signalling submission is adaptive in contests over low-value
38 resources. Our findings suggest that subordinate *N. pulcher* are primarily concerned with being
39 tolerated within the social group and may use submissive behaviour to avoid escalated conflict.
40 They offer a window into the factors that influence signals of submission in a highly social
41 vertebrate.

42 Keywords: aggression, contests, group living, *Neolamprologus pulcher*, social networks

43

44 In many species, individuals produce signals that appear to communicate submission during
45 agonistic interactions (Bernstein, 1981; Bradbury, & Vehrencamp, 2011; Huntingford, & Turner,
46 1987). These submissive behaviours can inhibit aggression in the receiving animal (Bernstein,

47 1981; Lorenz, 1966). For example, in contests between veiled chameleons, *Chamaeleo*
48 *calyptratus*, darkening body coloration leads to a rapid decrease in aggression by the receivers of
49 that signal and darkening is more likely when high levels of aggression are received (Ligon,
50 2014). Similarly, salmonid fishes (*Salmo* spp.) darken their body and eye coloration when giving
51 up in a contest (Hoglund, Balm, & Winberg, 2000; Keenleyside, & Yamamoto, 1962; O'Connor,
52 Metcalfe, & Taylor, 2000; Suter, & Huntingford, 2002), which inhibits further aggression in the
53 receiver and results in a precipitous decrease in attack intensity (O'Connor, Metcalfe, & Taylor,
54 1999). Much like the chameleons, the amount of aggression that the loser received in the contest
55 predicts the tendency to darken the body and submit (O'Connor et al., 1999).

56 Agonistic interactions are costly, requiring both time and energy, and can potentially
57 result in injury or death (for reviews see: Hardy, & Briffa, 2014; Huntingford, & Turner, 1987).
58 These costs may not be substantially different for the winner versus the loser of a contest
59 (Morrell, Lindstrom, & Ruxton, 2005), as both suffer opportunity costs, risk attracting predators
60 and reduce their vigilance (Jacobsson, Brick, & Kullberg, 1995). In general, the stress,
61 energetic costs and risk of injury during a contest are often similar for both participants (Brick,
62 1998; Copeland, Levay, Sivaraman, Beebe-Fugloni, & Earley, 2011; Earley, Edwards, Aseem,
63 Felton, Blumer, Karom, & Grober, 2006; Enquist, & Leimar 1990; Geist, 1974; Maan,
64 Groothuis, & Wittenberg, 2001). As a result, contestants share a mutual interest in minimizing
65 the costs associated with aggressive interactions (Maynard Smith, & Harper, 2003; Maynard
66 Smith, & Price, 1973). Therefore, despite being inherently competitive, fighting behaviour can
67 also contain elements of cooperation between the participants (Hurd, 1997).

68 Performing submissive displays may reduce the cost of conflict for both parties.
69 Signalling submission benefits the losing individual as it avoids further aggression, while the

70 winning individual also benefits, because by accepting this signal as an end to the conflict, it
71 prevents any more energy and time being wasted by continuing to attack and avoids the
72 possibility of injury or an upset (Bernstein, 1981). For example, pairs of fighting male crayfish,
73 *Procambarus clarkia*, perform less aggression overall, have lower fighting costs and a lower
74 probability of death if the loser submits by assuming a female-typical mating posture (Issa, &
75 Edwards, 2006). Compared to the vast literature on aggression, however, the factors that mediate
76 the use of submissive signals remain understudied. For a comprehensive understanding of the
77 evolution of animal contests both aggressive and submissive signalling need to be fully
78 considered (Ligon, 2014).

79 For animals living in complex social groups (e.g. cooperatively breeding species), some
80 level of conflict with other group members is unavoidable and often takes the form of aggressive
81 interactions (Aureli, & de Waal, 2000). Managing and dampening these within-group conflicts is
82 crucial for group stability (Aureli, Cords, & van Schaik, 2002; Kutsukake, & Clutton-Brock,
83 2008; Silk, 2007; de Waal, 1986). Therefore, group-living animals can face some unique costs of
84 conflict not shared by less social species because of a greater overlap in interests between
85 interacting parties. For example, many animal societies comprise related individuals with shared
86 inclusive fitness interests (Hamilton, 1964; West Eberhard, 1975; Lehmann, & Keller, 2006).
87 Even in the absence of relatedness, group productivity can contribute significantly to individual
88 fitness (Kokko, Johnstone, & Clutton-Brock, 2001). Therefore, competitors in group-living
89 animals may be especially likely to cooperate during an aggressive interaction (Balshine, Wong,
90 & Reddon, 2017). To understand the management and resolution of conflict within complex
91 social groups, it is crucial that we understand the factors that mediate the use of agonistic signals
92 during within-group interactions. Determining under what circumstances individual group

93 members are likely to show submissive behaviour may help us predict the structure of complex
94 groups (Kappeler, 2019; Peckre, Kappeler, & Fichtel, 2019).

95 *Neolamprologus pulcher* is a highly social, cooperatively breeding cichlid endemic to
96 Lake Tanganyika, Africa (Balshine-Earn, Neat, Reid, & Taborsky, 1998). It lives and breeds
97 within permanent social groups consisting of 3–20 adults (Balshine, Leach, Neat, Reid,
98 Taborsky, & Werner, 2001; Heg, Brouwer, Bachar, & Taborsky, 2005). These social groups are
99 organized as size-based linear dominance hierarchies: the largest male and female are socially
100 dominant and monopolize reproduction, while other group members act as nonreproductive
101 helpers and queue for breeding positions (Wong, & Balshine, 2011b). While rank is strongly
102 determined by body size within groups, body size at a given rank can vary across groups
103 depending on the group size and composition. Aggressive interactions are commonly observed
104 among group members including aggressive postures and displays (Fig. 1a) as well as physical
105 interactions such as ramming and biting (Dey, Reddon, O'Connor, & Balshine 2013; Reddon,
106 O'Connor, Marsh-Rollo, Balshine, Gozdowska, & Kulczykowska, 2015). A distinctive
107 submissive posture involves tilting the body axis upwards in the water column directing the
108 ventral body surface towards the receiver of the signal (Fig. 1b; Hick, Reddon, O'Connor, &
109 Balshine, 2014). This posture is often accompanied by a quivering of the tail or the entire body,
110 which may serve to increase the salience and intensity of the signal (Reddon et al., 2015).
111 Interestingly, the submissive posture appears to be the opposite form (or reverse mirror) of this
112 species' aggressive posture (head down in the water column (Fig. 1a), congruent with Darwin's
113 principle of antithesis (Hurd, Wachtmeister, & Enquist, 1995). Submissive behaviours are
114 typically shown in response to an aggressive action by a dominant fish (Hick et al., 2014;
115 Reddon, O'Connor, Marsh-Rollo, & Balshine, 2012). It has been suggested that submissive

116 behaviour is a key aspect of the social repertoire of this species (Balshine et al., 2017;
117 Bergmüller, & Taborsky, 2005; Fischer, Bohn, Oberhammer, Nyman, & Taborsky, 2017; Hick
118 et al., 2014; Taborsky, & Grantner, 1998) as this behaviour can facilitate acceptance of
119 subordinates within the group (Taborsky, Arnold, Junker, & Tschopp, 2012), which is essential
120 for their survival (Fischer, Zottl, Groenewoud, & Taborsky, 2014). Dominance interactions are
121 more common towards the top of the hierarchy, with highly ranked fish showing higher levels of
122 aggression (Dey, Reddon, O'Connor, & Balshine, 2013); however, individuals vary in how often
123 they produce agonistic displays (Dey et al., 2013; Reddon et al., 2012, 2015), and a better
124 understanding of what factors influence the use of submissive signals may help to clarify the
125 principles that determine the structure of social groups.

126 In this study, we used behavioural data collected previously on captive groups of *N.*
127 *pulcher* (Dey et al., 2013; Dey, Tan, O'Connor, Reddon, Caldwell, & Balshine, 2015) to
128 examine the factors influencing the use of submission signals. We predicted that submissive
129 behaviour would be more common when there are fewer places to flee to (Prediction 1) because
130 escape and submission are alternative tactics to avoid or terminate a conflict in this and other
131 species (Balshine et al., 2017; Ligon, 2014; Matsumura, & Hayden, 2006). We also predicted
132 that submission would be more frequent among competitors with a large difference in body size
133 and hence fighting ability, than in closely matched dyads (Prediction 2). This is because
134 relatively smaller fish face a heightened risk of injury (Lane, & Briffa, 2017) and are unlikely to
135 win if the contest escalates (Reddon, Voisin, Menon, Marsh-Rollo, Wong, & Balshine, 2011).
136 Alternatively, it is possible that fish close in size will have less certainty about their relative
137 fighting ability, thereby increasing the risk of an escalated conflict (Enquist, & Leimar, 1983),
138 and hence will have greater need for submission (Matsumura, & Hayden, 2006). We predicted

139 that submissive behaviour will be more common towards the bottom of the social hierarchy
140 (Prediction 3) because lower ranked fish may be more concerned with being tolerated in the
141 group and maintaining access to territory than competing for breeding positions (Wong, &
142 Balshine, 2011a, b) and therefore more willing to concede a conflict through submission. Finally,
143 we predicted that submission would be less common among same-sex pairs (Prediction 4)
144 because competition for breeding positions only occurs within the sexes and therefore conceding
145 to a same-sex opponent may be more costly. As above, an alternative prediction would be that
146 same-sex dyads will be in more acute conflict and therefore more likely to show submission to
147 avoid costly escalation.

148

149 <H1>METHODS

150 <H2>Study animals

151 The data for this study were collected in 2012 (Dey et al., 2013) and 2013 (Dey et al., 2015)
152 from a laboratory population of *N. pulcher* held at McMaster University, Hamilton, ON, Canada.
153 These fish were descendants of wild-caught *N. pulcher* from the Zambian coast of Lake
154 Tanganyika. Fish were housed in social groups of four to eight individuals composed of a
155 breeding pair and two to six mixed-sex helpers (mean group size in Dey et al., 2013 was 5.8
156 individuals, in Dey et al., 2015 it was 5.2 individuals) of varying body size. Each group occupied
157 a 189-litre (92 x 41 cm and 50 cm high) aquarium lined with 3 cm of coral sand substrate. Water
158 temperature was maintained at 26 ± 2 °C and the facility was kept on a 13:11 h light:dark cycle.
159 All groups were fed commercial cichlid flakes ad libitum, 6 days a week.

160 Prior to data collection, fish were given a unique fin clip (Dey et al., 2013) or
161 combination of fin clip and elastomer tag (Dey et al., 2015) to enable the unambiguous

162 identification of individuals in each group. Neither form of marking had apparent effects on
163 behaviour (see: Jungwirth, Balzarini, Zöttl, Salzmann, Taborsky, & Frommen, 2019; Stiver,
164 Dierkes, Taborsky, & Balshine, 2004) and fish resumed normal behaviour within 5 min of being
165 returned to their aquarium. All fish were sexed (by examination of their genital papillae) and
166 measured for standard length (the distance from the tip of the snout to the caudal peduncle, to the
167 nearest mm). Fish were assigned a rank, based on their relative size within their social group
168 (with rank = 1 indicating the largest individual). In *N. pulcher* groups, dominance rank is highly
169 dependent on body size (Taborsky, 1984, 1985; Wong & Balshine, 2011b) and rank was found to
170 be a key determinant of dominance behaviours in Dey et al. (2013, 2015).

171

172 <H2>Behavioural observations

173 Different fish in different social groups were used in each of the two studies. Fourteen social
174 groups were observed in each of the two previous studies; however, in one group from the Dey et
175 al., 2015 study, a ‘budding’ event occurred where a subordinate female established her own
176 territory within the aquarium and laid her own clutch during the study. Therefore, this group was
177 excluded from further analysis resulting in a final sample size of 27 groups for the current
178 analysis.

179 Each social group was observed for four 15 min periods for a total of 60 min of
180 observation per group. Observers sat 1.5 m from the focal aquaria and allowed the fish 5 min to
181 acclimate to their presence prior to beginning the 15 min observation period. Each behavioural
182 observation was conducted by a single observer who continually recorded all aggressive and
183 submissive interactions between pairs of individuals (for detailed ethograms see: Hick et al.,
184 2014; Reddon et al., 2015; Sopinka, Fitzpatrick, Desjardins, Stiver, Marsh-Rollo, & Balshine,

185 2009). The observer also recorded the identity of the actor and receiver in each interaction.
186 Although we recorded submissive behaviour in the previous studies, these data were only used to
187 compute dominance networks, and submission itself was not directly analysed.

188 In line with their different aims, the timing of behavioural observations differed slightly
189 between the two studies (see Table 1). In Dey et al. (2013), the groups were observed four times
190 over a period of 2 weeks. Analysis of the social networks showed that network structure was
191 highly consistent over time (i.e. across the four observation periods). In Dey et al. (2015), groups
192 were also observed four times, twice just after a reproductive event (0–3 days after eggs were
193 laid) and twice more 14–17 days after reproduction. Detailed analysis of the patterns of
194 dominance interactions in this second study also revealed a high degree of consistency in
195 interactions across time (i.e. we observed a similar network structure in the early parental care
196 and nonreproductive periods). The consistency suggests that any variation in patterns of
197 submissive behaviour is unlikely to be due to the differences in the timing of behavioural
198 observations across the two studies.

199 The only other difference between the two studies was in the availability of shelters in the
200 aquaria. In Dey et al. (2013), each group had access to two half terracotta flowerpots, which
201 acted as shelters (Fig. 2a). In Dey et al. (2015), each group again had access to two half terracotta
202 flowerpots and six black PVC tubes that served as additional shelters (Fig. 2b). We used this
203 difference in shelter availability between studies as an experimental treatment to test our first
204 prediction, that the opportunity to flee from aggression (provided by the extra shelter) would
205 reduce submissive behaviour. All other predictions were examined using a correlative approach
206 within social groups across studies.

207

208 <H2>Data analysis

209 All data analysis was conducted in R (R Core Team, 2017) using the statnet (Handcock, Hunter,
210 Butts, Goodreau, & Morris, 2008; Handcock, Hunter, Butts, Goodreau, Krivitsky, Bender-
211 deMoll, & Morris, 2016), ergm (Handcock, Hunter, Butts, Goodreau, Krivitsky, & Morris, 2017;
212 Hunter, Handcock, Butts, Goodreau, & Morris, 2008) and ergm.count (Krivitsky, 2016)
213 packages. Using this software, we built a network of submissive interactions based on the
214 behavioural data described above. Data from all four observation periods were pooled, and a
215 network for each social group was built with individual fish acting as nodes and the number of
216 submissive interactions between each dyad indicating the weight of ties between nodes. These
217 networks were directed, such that the tie representing the number of submissive interactions that
218 individual i performed towards individual j was specified separately from the tie representing the
219 number of submissive interactions from j to i (i.e. ties had directionality).

220 Next, we tested four predictions related to submissive behaviour (described above) using
221 exponential random graph models (ERGMs). ERGMs are a powerful tool for analysis of social
222 networks (Lusher, Koskinen, & Robins, 2013; Silk, & Fisher, 2017) and are somewhat analogous
223 to generalized linear models. They allow observed networks to act as ‘response’ variables, while
224 multiple individual, dyad level or structural traits can be included as ‘predictor’ variables. The
225 models then aim to test whether (and how strongly) the predictor variables predict the presence
226 (or weight) of ties in the observed network, as compared to null models.

227 Prior to constructing ERGMs for this study, we first built a supernetwork of submissive
228 interactions so that we could fit a single ERGM to our empirical data set (i.e. all 27 social
229 groups). This supernetwork was created by combining the submissive networks from the 27
230 social groups into one network object (see Results; Dey, & Quinn, 2014) and was both weighted

231 (i.e. ties between nodes had value) and directed (i.e. ties between nodes had directionality). We
232 restricted the randomized networks computed by the ERGM fitting process (i.e. the distribution
233 of possible networks) to only allow ties within social groups.

234 Next, we a priori chose the set of predictor variables that would test our four predictions
235 while also controlling for confounds in the network structure. These predictor variables were as
236 follows: (1) effect of shelter availability (with values of ‘high’ or ‘low’), which tests whether
237 submission is related to the availability of shelters (Prediction 1); (2) effect of size differences
238 ($\log(\text{standard length A}/\text{standard length B})$), which tests whether submission is dependent on size
239 asymmetry among dyads (Prediction 2); (3) effect of rank, which tests whether high- or low-
240 ranking individuals are more likely to produce submissive displays (Prediction 3); and (4) sexual
241 homophily, which tests whether submission is more, or less, likely in interactions among same-
242 sex dyads (Prediction 4).

243
244 To control for confounding factors, we also included several variables related to the structure of
245 submissive networks in *N. pulcher*: (5) the ‘sum’ term, which is analogous to an intercept in a
246 linear model and controls for the mean level of submissive interactions among individuals,
247 ensures that the null models produced in the ERGM fitting process have the same total number
248 of submissive interactions as the empirical data; (6) the ‘nonzero’ term accounts for inflation in
249 the number of noninteracting pairs compared to the underlying reference models (Poisson in this
250 case, see below); (7) the number of aggressive interactions received by an individual controls for
251 the amount of aggression received when analysing patterns of submissive behaviour; and (8)
252 effect of the difference in rank controls for rank differences between the actor and receiver,
253 which are a strong driver of overall patterns of dominance interactions (Dey et al., 2013).

254

255 Since the response variable was count data (number of submissive displays), the model was
256 fitted using a Poisson reference graph. Visual analysis of Markov chain Monte Carlo sample
257 statistics from this model, as well as networks simulated from the fitted model, did not show any
258 evidence of degeneracy (Handcock, 2003; Handcock, Robins, Snijders, Moody, & Besag, 2003).
259 Additionally, models were checked for goodness of fit by examining the distributions of nodal
260 strength (i.e. weighted degree) from 100 simulated networks from the model and comparing
261 these distributions to the observed network (see also Goodreau, Kits, & Morris, 2009). The code
262 and data required to recreate this model are available on Mendeley Data. The figures in this
263 paper were created using the ggplot2 (Wickham, 2016), ggridges (Claus, & Wilke, 2018) and
264 arcdiagram (Sanchez, 2014) packages. Code for reproducing the figures is available upon
265 request.

266

267 <H2>*Ethical note*

268 Animal housing, handling and study protocols were approved by the McMaster Animal
269 Research Ethics Board (Animal Utilization Protocol 10-11-71) and adhered to the guidelines of
270 the Canadian Council for Animal Care. Fish were marked with dorsal fin clips using a sharp pair
271 of scissors to remove a single fin ray and/or a small visible elastomer implant injected beneath
272 the skin. Neither of these marking methods causes any apparent long-term distress to the fish.
273 All fish were monitored closely throughout the study and would have been removed from their
274 social groups if we had seen eviction from the social group or evidence of injury, but this did not
275 occur. Four fish died of unknown causes and these individuals were removed from all their
276 networks.

277

278 <H1>RESULTS

279 We found that fish with greater access to shelters were less submissive than fish with little access
280 to shelters (Prediction 1; Table 2, Fig. 3). Submission was more common when size asymmetry
281 was high (Prediction 2; Table 2, Fig. 4), and high-ranking individuals were less likely to produce
282 submission signals (Prediction 3; Table 2, Fig. 5a), even after we controlled for important
283 confounds such as the amount of aggression received (Table 2, Fig. 5b). Finally, we found that
284 submission signals were more likely towards opposite-sex than same-sex groupmates (Prediction
285 4; Table 2, Fig. 5a, b).

286

287 <H1>DISCUSSION

288 We applied a social network approach to analyse detailed behavioural observations collected on
289 27 laboratory-housed social groups of the cooperatively breeding cichlid fish *N. pulcher* and
290 found that, in accordance with our predictions, a greater number of available shelters (and hence
291 the potential to escape aggression) reduced the tendency to show submissive displays (Prediction
292 1). Also fitting with our prediction, individuals of lower rank submitted more often even after we
293 controlled for the possibility that lower ranked fish may receive more aggression as a result of
294 having more fish above them in the hierarchy (Prediction 3). We found that individuals were
295 more likely to show submission in opposite-sex than same-sex dyads, in line with Prediction 4.
296 Finally, as predicted, fish that were much smaller than the individual they were interacting with
297 were more likely to show submission (Prediction 2).

298 We found that greater shelter availability decreased the likelihood of submissive displays
299 (Prediction 1). Theoretical and empirical work suggests that submission should be more common

300 when the opportunity to flee from an aggressor is limited by physical or ecological restrictions
301 on escape (Ligon, 2014; Matsumura, & Hayden, 2006), and fleeing and submission are
302 negatively correlated in *N. pulcher* (Balshine et al., 2017). Our results fit with this framework:
303 when subordinate *N. pulcher* had more shelters available in their territory they were less likely to
304 show submission, presumably because they could escape, take refuge or avoid aggression more
305 easily. We would predict that natural *N. pulcher* groups with more members or fewer shelters
306 would exhibit higher levels of submission than smaller groups or groups with more shelters in
307 their territory. Groups that are closer to the periphery of the colony (Brown, & Brown, 1987;
308 Forster, & Phillips, 2009; Hellmann, Ligoeki, O'Connor, Reddon, Garvy, Marsh-Rollo, Gibbs,
309 Balshine, & Hamilton, 2015) or in areas with more risk from predation (Groenewoud, Frommen,
310 Josi, Tanaka, Jungwirth, & Taborsky, 2016) may be more likely to show submission because
311 these factors may increase the costs of fleeing behaviour.

312 The effect of shelter number on submission that we detected could be the result of
313 drawing different shelter treatments from two different studies each with different original
314 objectives and slightly different protocols. While both studies took place in the same laboratory,
315 with the same observational techniques and using the same population of fish (but not the same
316 individuals), it remains possible that slight differences in the procedure could have resulted in the
317 differences in submissive behaviour that we detected. We think this unlikely, given the similarity
318 in protocols, but this result should be confirmed in future studies. The use of the two data sets
319 was not an issue for any of our other results, as all other predictions (Predictions 2–4) drew
320 inferences from across the two studies rather than by comparing them directly.

321 Our observations show that submissive behaviour is most often used by small, low-
322 ranking fish (Predictions 2–3). These individuals may be primarily concerned with being

323 tolerated in the group in order to secure the protection from predation that group membership
324 provides (Heg, Bachar, Brouwer, & Taborsky, 2004; Tanaka, Frommen, Takahashi, & Kohda,
325 2016; Groenewoud et al., 2016), and perhaps less concerned with conflicts over social status
326 (Wong, & Balshine, 2011b). Similarly, subordinate house mice, *Mus musculus domesticus*, use
327 scent to indicate their status to dominant territory owners and increase the degree to which they
328 are tolerated in the territory of the dominant male (Hurst, Fang, & Barnard, 1993). By acting
329 submissively, low-ranking *N. pulcher* are more accepted by dominant group members
330 (Bergmüller, & Taborsky, 2005; Taborsky et al., 2012). By contrast, in meerkats, *Suricata*
331 *suricatta*, older and higher ranking subordinate females are more submissive to the breeding
332 female but are nevertheless more likely to be evicted than younger, less submissive individuals
333 (Kutsukake, & Clutton-Brock, 2008). Subordinate *N. pulcher* show more submissive behaviour
334 after being temporarily removed from the group (Balshine-Earn et al., 1998), which suggests an
335 increased motivation to reintegrate themselves into the hierarchy and perhaps to pre-empt
336 dominant aggression resulting from an apparent dereliction of cooperative duties (Bergmüller, &
337 Taborsky 2005; Fischer et al., 2014). Because their natural predators are gape limited (Heg et al.,
338 2004), smaller fish are more vulnerable and therefore may be more willing to show submission
339 to maintain the safety conferred by group membership.

340 We found that *N. pulcher* dyads that were disparate in body size were more likely to
341 show submissive behaviours (Prediction 2). Body size is a strong determinant of fighting ability
342 across the animal kingdom, and much smaller contestants have a low likelihood of success in
343 most species (Parker, 1974). Reddon et al. (2011) found that when *N. pulcher* pairs that differed
344 in body size by 5% or more came into conflict, the larger individual nearly always emerged
345 victorious, suggesting that relatively smaller fish are unlikely to succeed in a contest. This

346 finding also fits with the suggestion that low-value conflicts tend to end with submission. A fish
347 that is much smaller than its opponent has a low likelihood of success and the value placed on
348 that chance may be small. Smaller and weaker animals may also face greater injury risk when
349 attacked by larger and stronger animals (Lane, & Briffa, 2017) increasing the potential costs of
350 the interaction.

351 Alternatively, it is conceivable that individuals that are close in body size may be in more
352 intense conflict and therefore have greater need for submissive behaviour. Supportive of this
353 notion and in contrast to our results, previous work on experimental *N. pulcher* groups in the
354 laboratory has shown that when the breeder male is relatively close in size to the largest male
355 subordinate in that group, the subordinate tends to show more submission overall (Hamilton,
356 Heg, & Bender, 2005). However, these closely matched fish are also likely to interact more often
357 in general (Dey et al., 2013). Our results account for the higher rate of aggressive interactions
358 between closely matched individuals, and show that on a per aggressive act basis, fish that are
359 close in size are less likely to show submission. In their game theoretic model of submissive
360 behaviour, Matsumura and Hayden (2006) also predicted that closely matched opponents should
361 be more likely to show submission, but their model assumed that the dominant animal in a highly
362 asymmetric dyad would ignore submissive displays from the smaller animal and continue to
363 attack. Anecdotally, this does describe the behaviour we observed in stable *N. pulcher* groups,
364 although a detailed analysis of the sequencing of aggressive and submissive behaviours within
365 these groups would be necessary to clarify this issue.

366 We also found that *N. pulcher* were more likely to show submission in response to
367 aggression from an opposite-sex than a same-sex group member (Prediction 4). Because the
368 queue for a dominant breeding position is sex specific, establishing or maintaining status

369 relationships with members of the opposite sex is less important for lifetime fitness prospects
370 (Stiver, Fitzpatrick, Desjardins, & Balshine, 2006). We interpret the greater use of submissive
371 behaviour in intersexual interactions as support for the idea that submission is more likely in
372 low-value contests (Matsumura, & Hayden, 2006).

373 In conclusion, we found that submissive behaviour was common within *N. pulcher* social
374 groups. It was observed more often in groups with less access to shelters and thus fewer places to
375 escape aggression and in individuals that were substantially smaller than and were of the
376 opposite sex to the receiving animal. Fish of a low rank within the group were also more likely to
377 show submission than higher ranked fish. Submissive displays appear to be a key aspect of the
378 behavioural repertoire of this highly social species. They may allow groupmates to resolve
379 conflicts without the need to flee from the safety of the social group. Submissive behaviour may
380 be a particularly important adaptation for animals living in complex social groups which must
381 frequently interact with their groupmates while having only a limited ability to flee from conflict
382 because of social or ecological constraints.

383

384 **Author contributions**

385 A.R. conceived the study. C.D. conducted the analysis and prepared the figures. A.R. wrote the
386 first draft of the manuscript. All authors contributed to the final version.

387

388 **Data availability**

389 The complete data set and code required to recreate the analysis are available on Mendeley Data
390 (<https://data.mendeley.com/>).

391 **Acknowledgments**

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396

397

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683

684 **Figure captions**

685 **Figure 1.** (a) The head-down threat posture of *Neolamprologus pulcher*: a typical aggressive
686 display that is often accompanied by a flaring of the opercula. (b) The head-up submissive
687 posture of *N. pulcher* with commonly co-occurring rapid quivering of the tail.

688

689 **Figure 2.** A depiction of the social group housing aquaria used in this study. (a) Fourteen groups
690 were provided with two half terracotta flowerpots to be used as shelters and breeding substrate.
691 (b) Thirteen groups had the same two terracotta pots as well as six additional opaque PVC pipes
692 for shelter, thereby increasing the opportunity for subordinate fish to flee from aggression.

693

694 **Figure 3.** Number of submissive interactions in a 1 h period for *N. pulcher* dyads as a function of
695 shelter availability: (a) many shelters; (b) few shelters. The mean number of submissive
696 interactions is shown with an orange dashed line. Only dyads that could possibly interact (i.e.
697 were in the same social group) are included in this analysis ($N = 395$ dyads).

698

699 **Figure 4.** Number of submissive interactions in a 1 h period as a function of body size
700 asymmetry (difference in $\log(\text{standard length})$) for all dyads across 27 *N. pulcher* social groups
701 ($N = 144$ individuals). Only dyads that could possibly interact (i.e. were in the same social
702 group) are shown ($N = 395$ dyads). A linear fit (with SE represented by the shaded grey area) is
703 shown for plotting purposes only (see Table 2 for details of statistical analysis).

704

705 **Figure 5.** Arc diagram (i.e. a one-dimensional network diagram) of (a) submissive interactions
706 and (b) the ratio of submissive interactions to aggressive interactions within *N. pulcher* social

707 groups. Each node (filled circles positioned along the x-axis) represents a single fish with the
708 colour of the node indicating the rank of that fish within its social group ($N=144$ fish from 27
709 social groups). Arcs between nodes represent interactions between fish, with the size of the arc
710 representing (a) the number of submissive interactions and (b) the ratio of submissive
711 interactions given to aggressive interactions received. Arc colour indicates the rank of the
712 submissive individual. Arcs positioned above the nodes indicate interactions among opposite-sex
713 dyads, while arcs positioned below the nodes indicate same-sex interactions. Cichlid images
714 courtesy of Milton Tan ([Creative commons licence BY-NC-SA 3.0](#)).

715

716

717 Table 1. Summary of the combined data sets analysed in this study

	Dey et al. (2013)	Dey et al. (2015)/
Number of social groups	14	13
Number of observations	4	4
Length of preobservation acclimation (min)	5	5
Length of each observation period (min)	15	15
Behaviours recorded	Aggressive and submissive	Aggressive and submissive
Total aggressive interactions observed	1474	1460
Total submissive interactions observed	1200	890
Shelters available	2 half flower pots	2 half flower pots + 6 PVC tubes
Timing of observation periods	2 per week for 2 weeks (never more than 1 observation per day).	2 observations within the first 0–3 days after reproduction + 2 observations 14–17 days after reproduction (never more than 1 observation per day)

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722 **Table 2.** Results of exponential random graph modelling of submissive behaviour in 27 social
 723 groups of *N. pulcher*

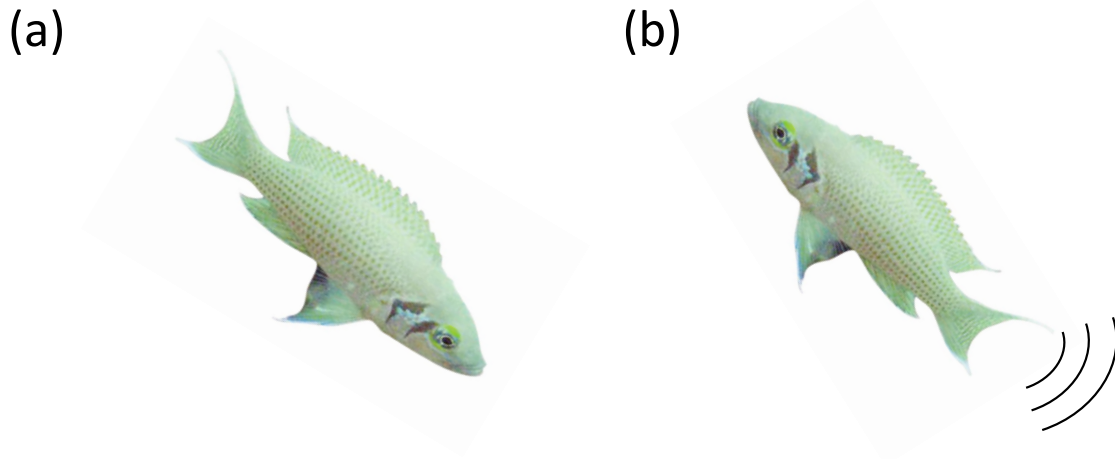
Predictor variables	Estimate	SE	P
Shelter availability [high]	-0.045	0.013	< 0.001
Difference in body size	0.185	0.070	0.009
Actor's rank	0.063	0.008	< 0.001
Sexual homophily	-0.054	0.025	0.033
Sum	1.583	0.054	< 0.001
Non-zero	-7.551	0.213	< 0.001
Aggressive interactions received	0.029	0.002	< 0.001
Difference in rank	0.014	0.012	0.231

724

725

726

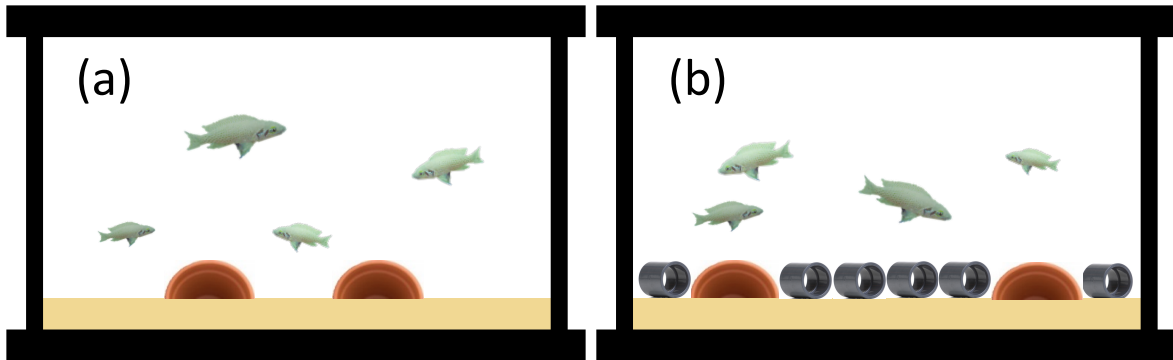
727 **Figure 1**



728

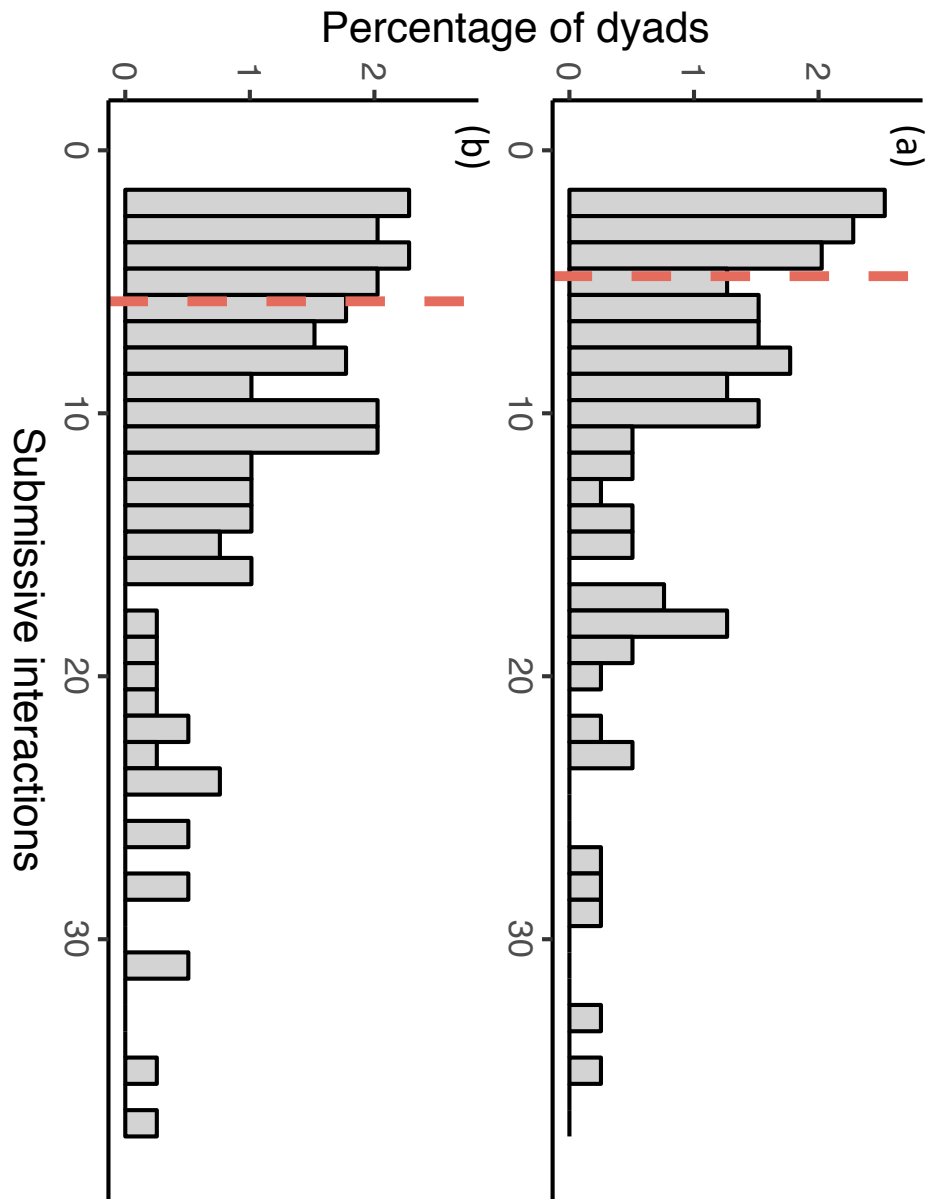
729

730 **Figure 2**

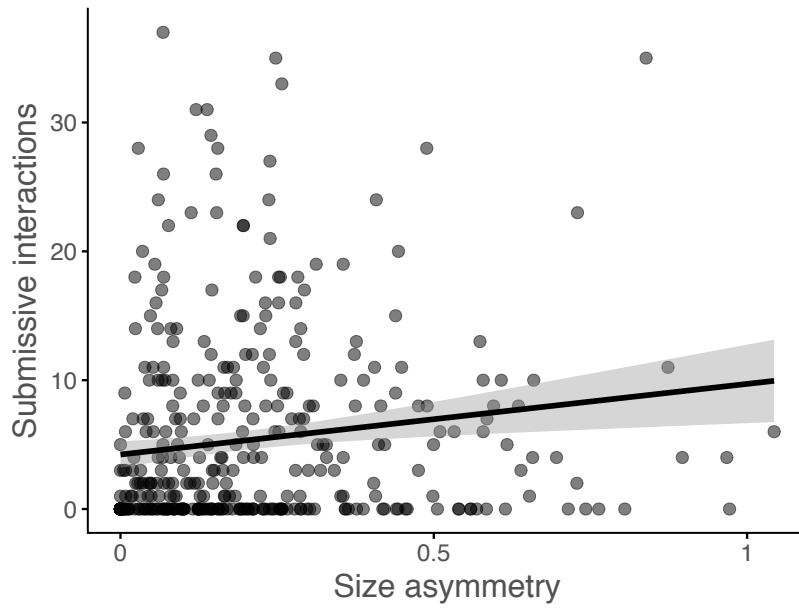


731

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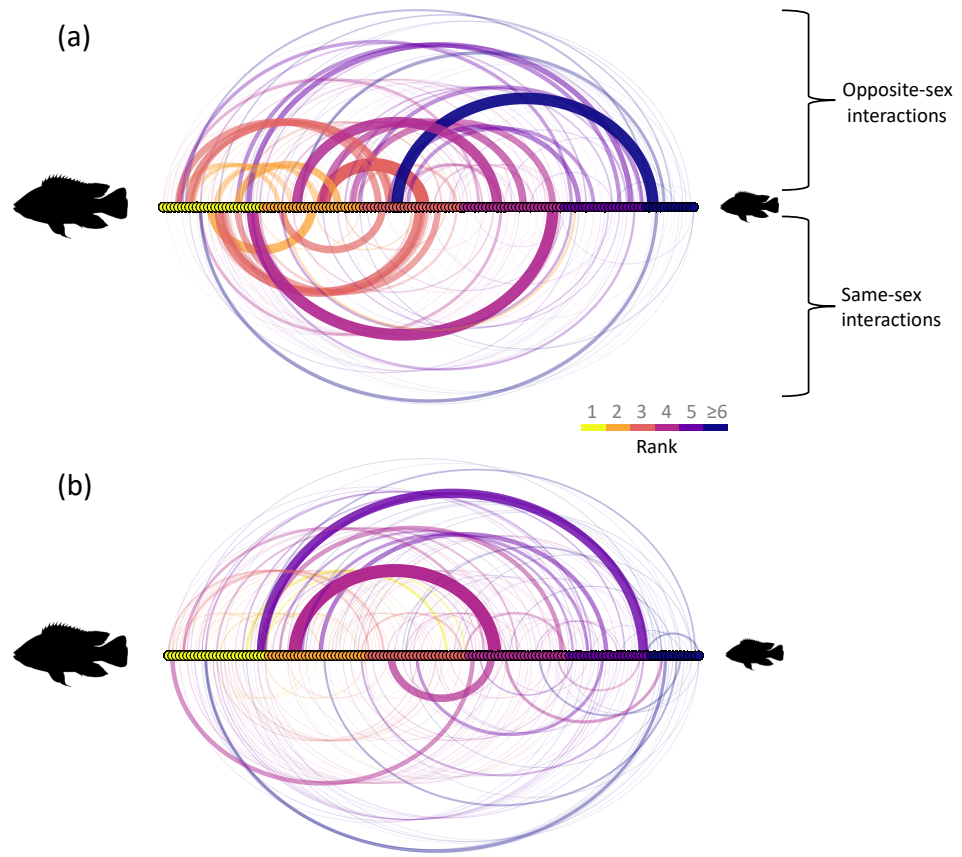
736 **Figure 4**



737

738

739 **Figure 5**



740