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

Adam R Reddon[1*], Cody J Dey[2], Sigal Balshine[3]

[1] *School of Natural Sciences and Psychology, Liverpool John Moores University, Liverpool, U.K.*

[2] *Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON, Canada*

[3] *Department of Psychology, Neuroscience & Behaviour, McMaster University, Hamilton, ON, Canada*

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*Correspondence: A. R. Reddon, *School of Natural Sciences and Psychology, Liverpool John Moores University, James Parsons Building, Byrom Street, Liverpool L3 3AF, U.K.*
E-mail address: a.r.reddon@ljmu.ac.uk

Acting submissively may inhibit aggression and facilitate the termination of contests without further escalation. The need to minimize conflict is vital in highly social species where within-group interactions are frequent, and aggression can dampen group productivity. Within social groups, individual group members may modulate their use of submissive signals depending on their phenotype, the value of the contested resource, their relationship to the receiver of the signal and the characteristics of the local environment. We predicted that submissive behaviour would be more common when signallers had limited ability to flee from conflict, when signallers were of a low rank within the group, when signallers and receivers differed substantially in body size (and thus in fighting ability), and when signallers and receivers were of opposite sex and therefore not directly in competition over reproductive opportunities. We tested these predictions using social network analyses on detailed behavioural observations from 27 social groups of the cooperatively breeding cichlid fish *Neolamprologus pulcher*. Congruent with our prediction, submissive behaviour was more common when there were fewer shelters available, suggesting that constraints on fleeing behaviour may increase the use of submission. Also fitting with predictions, submissive behaviour was more common with increasing body size asymmetry between the competitors, among lower ranked fish and in interactions between opposite-sex dyads, which supports the idea that signalling submission is adaptive in contests over low-value resources. Our findings suggest that subordinate *N. pulcher* are primarily concerned with being tolerated within the social group and may use submissive behaviour to avoid escalated conflict. They offer a window into the factors that influence signals of submission in a highly social vertebrate.

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

In many species, individuals produce signals that appear to communicate submission during agonistic interactions (Bernstein, 1981; Bradbury, & Vehrencamp, 2011; Huntingford, & Turner, 1987). These submissive behaviours can inhibit aggression in the receiving animal (Bernstein, 1981; Lorenz, 1966). For example, in contests between veiled chameleons, *Chamaeleo calyptratus*, darkening body coloration leads to a rapid decrease in aggression by the receivers of that signal and darkening is more likely when high levels of aggression are received (Ligon, 2014). Similarly, salmonid fishes (*Salmo* spp.) darken their body and eye coloration when giving up in a contest (Hoglund, Balm, & Winberg, 2000; Keenleyside, & Yamamoto, 1962; O'Connor, Metcalfe, & Taylor, 2000; Suter, & Huntingford, 2002), which inhibits further aggression in the receiver and results in a precipitous decrease in attack intensity (O'Connor, Metcalfe, & Taylor, 1999). Much like the chameleons, the amount of aggression that the loser received in the contest predicts the tendency to darken the body and submit (O'Connor et al., 1999).

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

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

For animals living in complex social groups (e.g. cooperatively breeding species), some level of conflict with other group members is unavoidable and often takes the form of aggressive interactions (Aureli, & de Waal, 2000). Managing and dampening these within-group conflicts is crucial for group stability (Aureli, Cords, & van Schaik, 2002; Kutsukake, & Clutton-Brock, 2008; Silk, 2007; de Waal, 1986). Therefore, group-living animals can face some unique costs of conflict not shared by less social species because of a greater overlap in interests between interacting parties. For example, many animal societies comprise related individuals with shared inclusive fitness interests (Hamilton, 1964; West Eberhard, 1975; Lehmann, & Keller, 2006). Even in the absence of relatedness, group productivity can contribute significantly to individual fitness (Kokko, Johnstone, & Clutton-Brock, 2001). Therefore, competitors in group-living animals may be especially likely to cooperate during an aggressive interaction (Balshine, Wong, & Reddon, 2017). To understand the management and resolution of conflict within complex social groups, it is crucial that we understand the factors that mediate the use of agonistic signals during within-group interactions. Determining under what circumstances individual group members are likely to show submissive behaviour may help us predict the structure of complex groups (Kappeler, 2019; Peckre, Kappeler, & Fichtel, 2019).

Neolamprologus pulcher is a highly social, cooperatively breeding cichlid endemic to Lake Tanganyika, Africa (Balshine-Earn, Neat, Reid, & Taborsky, 1998). It lives and breeds within permanent social groups consisting of 3–20 adults (Balshine, Leach, Neat, Reid, Taborsky, & Werner, 2001; Heg, Brouwer, Bachar, & Taborksy, 2005). These social groups are organized as size-based linear dominance hierarchies: the largest male and female are socially dominant and monopolize reproduction, while other group members act as nonreproductive helpers and queue for breeding positions (Wong, & Balshine, 2011b). While rank is strongly determined by body size within groups, body size at a given rank can vary across groups depending on the group size and composition. Aggressive interactions are commonly observed among group members including aggressive postures and displays (Fig. 1a) as well as physical interactions such as ramming and biting (Dey, Reddon, O'Connor, & Balshine 2013; Reddon, O'Connor, Marsh-Rollo, Balshine, Gozdowska, & Kulczykowska, 2015). A distinctive submissive posture involves tilting the body axis upwards in the water column directing the ventral body surface towards the receiver of the signal (Fig. 1b; Hick, Reddon, O'Connor, & Balshine, 2014). This posture is often accompanied by a quivering of the tail or the entire body, which may serve to increase the salience and intensity of the signal (Reddon et al., 2015). Interestingly, the submissive posture appears to be the opposite form (or reverse mirror) of this species' aggressive posture (head down in the water column (Fig. 1a), congruent with Darwin's principle of antithesis (Hurd, Wachtmeister, & Enquist, 1995). Submissive behaviours are typically shown in response to an aggressive action by a dominant fish (Hick et al., 2014; Reddon, O'Connor, Marsh-Rollo, & Balshine, 2012). It has been suggested that submissive behaviour is a key aspect of the social repertoire of this species (Balshine et al., 2017; Bergmüller, & Taborsky, 2005; Fischer, Bohn, Oberhummer, Nyman, & Taborksy, 2017; Hick et al., 2014; Taborsky, & Grantner, 1998) as this behaviour can facilitate acceptance of subordinates within the group (Taborsky, Arnold, Junker, & Tschopp, 2012), which is essential for their survival (Fischer, Zottl, Groenewoud, & Taborsky, 2014). Dominance interactions are more common towards the top of the hierarchy, with highly ranked fish showing higher levels of aggression (Dey, Reddon, O'Connor, & Balshine, 2013); however, individuals vary in how often they produce agonistic displays (Dey et al., 2013; Reddon et al., 2012, 2015), and a better understanding of what factors influence the use of submissive signals may help to clarify the principles that determine the structure of social groups.

In this study, we used behavioural data collected previously on captive groups of *N. pulcher* (Dey et al., 2013; Dey, Tan, O'Connor, Reddon, Caldwell, & Balshine, 2015) to examine the factors influencing the use of submission signals. We predicted that submissive behaviour would be more common when there are fewer places to flee to (Prediction 1) because escape and submission are alternative tactics to avoid or terminate a conflict in this and other species (Balshine et al., 2017; Ligon, 2014; Matsumura, & Hayden, 2006). We also predicted that submission would be more frequent among competitors with a large difference in body size and hence fighting ability, than in closely matched dyads (Prediction 2). This is because relatively smaller fish face a heightened risk of injury (Lane, & Briffa, 2017) and are unlikely to win if the contest escalates (Reddon, Voisin, Menon, Marsh-Rollo, Wong, & Balshine, 2011). Alternatively, it is possible that fish close in size will have less certainty about their relative fighting ability, thereby increasing the risk of an escalated conflict (Enquist, & Leimar, 1983), and hence will have greater need for submission (Matsumura, & Hayden, 2006). We predicted that submissive behaviour will be more common towards the bottom of the social hierarchy (Prediction 3) because lower ranked fish may be more concerned with being tolerated in the group and maintaining access to territory than competing for breeding positions (Wong, & Balshine, 2011a, b) and therefore more willing to concede a conflict through submission. Finally, we predicted that submission would be less common among same-sex pairs (Prediction 4) because competition for breeding positions only occurs within the sexes and therefore conceding to a same-sex opponent may be more costly. As above, an alternative prediction would be that same-sex dyads will be in more acute conflict and therefore more likely to show submission to avoid costly escalation.

<H1>METHODS

<H2>Study animals

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

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

<H2>Behavioural observations

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

Each social group was observed for four 15 min periods for a total of 60 min of observation per group. Observers sat 1.5 m from the focal aquaria and allowed the fish 5 min to acclimate to their presence prior to beginning the 15 min observation period. Each behavioural observation was conducted by a single observer who continually recorded all aggressive and submissive interactions between pairs of individuals (for detailed ethograms see: Hick et al., 2014; Reddon et al., 2015; Sopinka, Fitzpatrick, Desjardins, Stiver, Marsh-Rollo, & Balshine, 2009). The observer also recorded the identity of the actor and receiver in each interaction. Although we recorded submissive behaviour in the previous studies, these data were only used to compute dominance networks, and submission itself was not directly analysed.

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

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

<H2>Data analysis

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

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

Prior to constructing ERGMs for this study, we first built a supernetwork of submissive interactions so that we could fit a single ERGM to our empirical data set (i.e. all 27 social groups). This supernetwork was created by combining the submissive networks from the 27 social groups into one network object (see Results; Dey, & Quinn, 2014) and was both weighted (i.e. ties between nodes had value) and directed (i.e. ties between nodes had directionality). We restricted the randomized networks computed by the ERGM fitting process (i.e. the distribution of possible networks) to only allow ties within social groups.

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

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

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

<H2>*Ethical note*

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

<H1>RESULTS

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

<H1>DISCUSSION

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

We found that greater shelter availability decreased the likelihood of submissive displays (Prediction 1). Theoretical and empirical work suggests that submission should be more common when the opportunity to flee from an aggressor is limited by physical or ecological restrictions on escape (Ligon, 2014; Matsumura, & Hayden, 2006), and fleeing and submission are negatively correlated in *N. pulcher* (Balshine et al., 2017). Our results fit with this framework: when subordinate *N. pulcher* had more shelters available in their territory they were less likely to show submission, presumably because they could escape, take refuge or avoid aggression more easily. We would predict that natural *N. pulcher* groups with more members or fewer shelters would exhibit higher levels of submission than smaller groups or groups with more shelters in their territory. Groups that are closer to the periphery of the colony (Brown, & Brown, 1987; Forster, & Phillips, 2009; Hellmann, Ligocki, O'Connor, Reddon, Garvy, Marsh-Rollo, Gibbs, Balshine, & Hamilton, 2015) or in areas with more risk from predation (Groenewoud, Frommen, Josi, Tanaka, Jungwirth, & Taborsky, 2016) may be more likely to show submission because these factors may increase the costs of fleeing behaviour.

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

Our observations show that submissive behaviour is most often used by small, low-ranking fish *(*Predictions 2–3). These individuals may be primarily concerned with being tolerated in the group in order to secure the protection from predation that group membership provides (Heg, Bachar, Brouwer, & Taborsky, 2004; Tanaka, Frommen, Takahashi, & Kohda, 2016; Groenewoud et al., 2016), and perhaps less concerned with conflicts over social status (Wong, & Balshine, 2011b). Similarly, subordinate house mice, *Mus musculus domesticus*, use scent to indicate their status to dominant territory owners and increase the degree to which they are tolerated in the territory of the dominant male (Hurst, Fang, & Barnard, 1993). By acting submissively, low-ranking *N. pulcher* are more accepted by dominant group members (Bergmüller, & Taborsky, 2005; Taborksy et al., 2012). By contrast, in meerkats, *Suricata suricatta*, older and higher ranking subordinate females are more submissive to the breeding female but are nevertheless more likely to be evicted than younger, less submissive individuals (Kutsukake, & Clutton-Brock, 2008). Subordinate *N. pulcher* show more submissive behaviour after being temporarily removed from the group (Balshine-Earn et al., 1998), which suggests an increased motivation to reintegrate themselves into the hierarchy and perhaps to pre-empt dominant aggression resulting from an apparent dereliction of cooperative duties (Bergmüller, & Taborsky 2005; Fischer et al., 2014). Because their natural predators are gape limited (Heg et al., 2004), smaller fish are more vulnerable and therefore may be more willing to show submission to maintain the safety conferred by group membership.

We found that *N. pulcher* dyads that were disparate in body size were more likely to show submissive behaviours (Prediction 2). Body size is a strong determinant of fighting ability across the animal kingdom, and much smaller contestants have a low likelihood of success in most species (Parker, 1974). Reddon et al. (2011) found that when *N. pulcher* pairs that differed in body size by 5% or more came into conflict, the larger individual nearly always emerged victorious, suggesting that relatively smaller fish are unlikely to succeed in a contest. This finding also fits with the suggestion that low-value conflicts tend to end with submission. A fish that is much smaller than its opponent has a low likelihood of success and the value placed on that chance may be small. Smaller and weaker animals may also face greater injury risk when attacked by larger and stronger animals (Lane, & Briffa, 2017) increasing the potential costs of the interaction.

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

We also found that *N. pulcher* were more likely to show submission in response to aggression from an opposite-sex than a same-sex group member (Prediction 4). Because the queue for a dominant breeding position is sex specific, establishing or maintaining status relationships with members of the opposite sex is less important for lifetime fitness prospects (Stiver, Fitzpatrick, Desjardins, & Balshine, 2006). We interpret the greater use of submissive behaviour in intersexual interactions as support for the idea that submission is more likely in low-value contests (Matsumura, & Hayden, 2006).

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

Author contributions

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

Data availability

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

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Figure captions

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

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

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

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

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

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

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)

Table 2. Results of exponential random graph modelling of submissive behaviour in 27 social 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

Figure 1

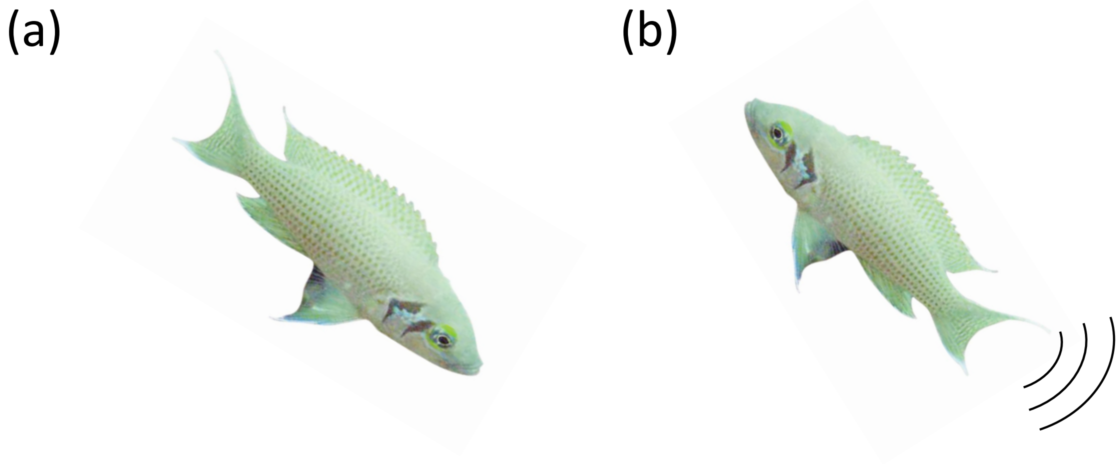


Figure 2

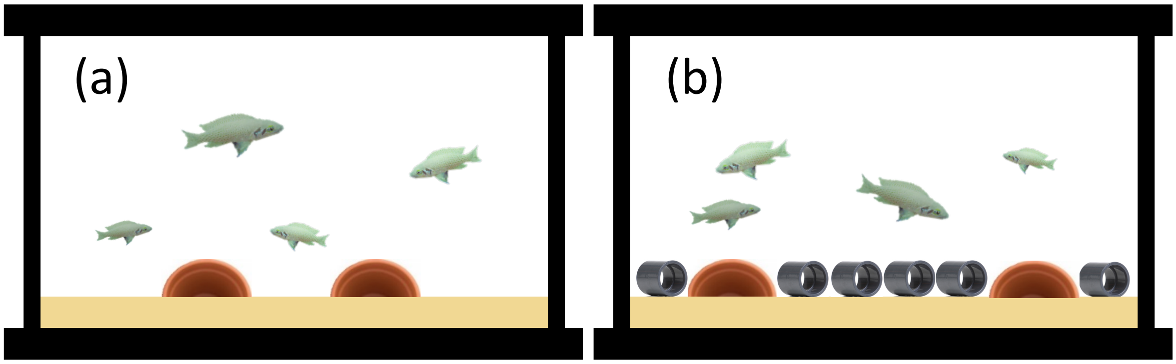
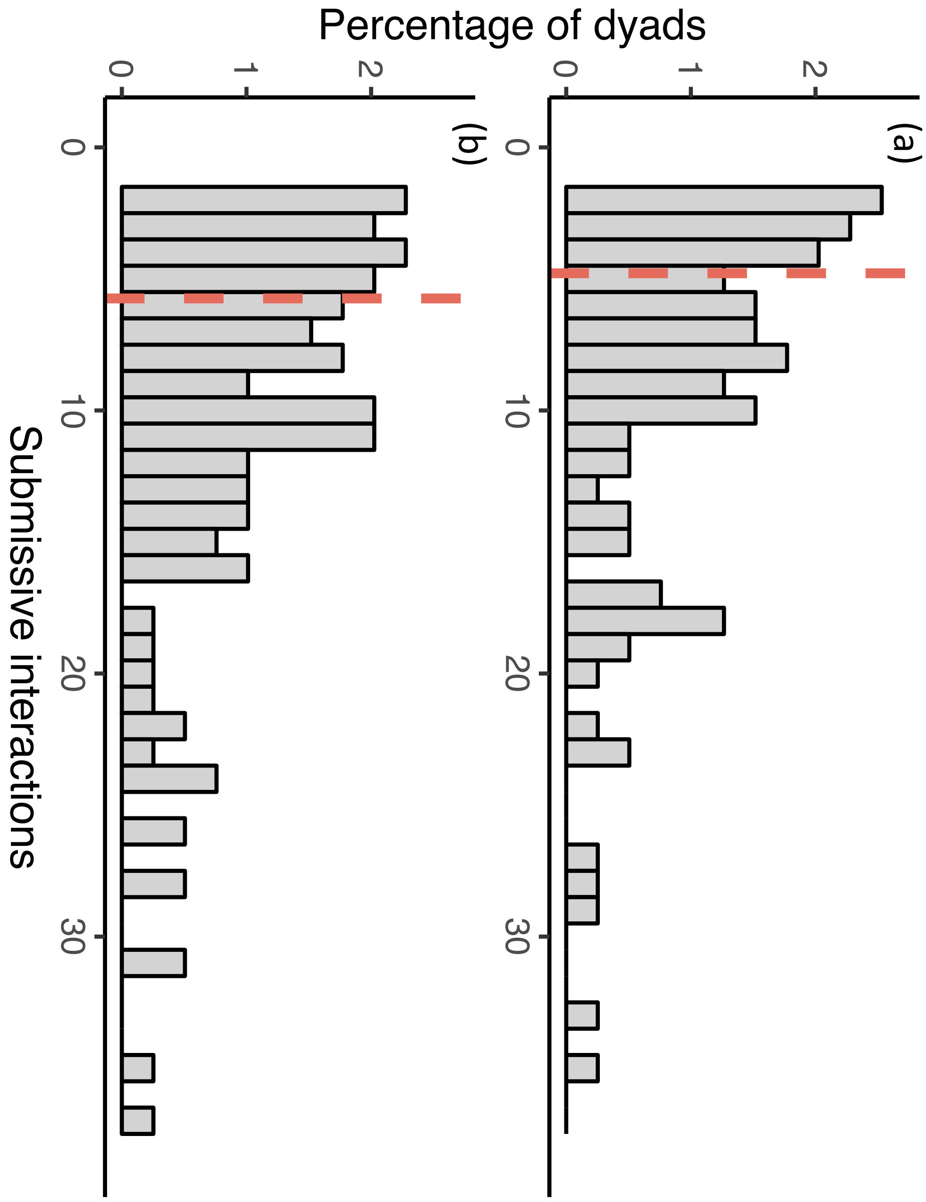


Figure 3



Percentage of dyads
(a)
(b)
0
1
2
0
10
20
30
Submissive interactions

Figure 4

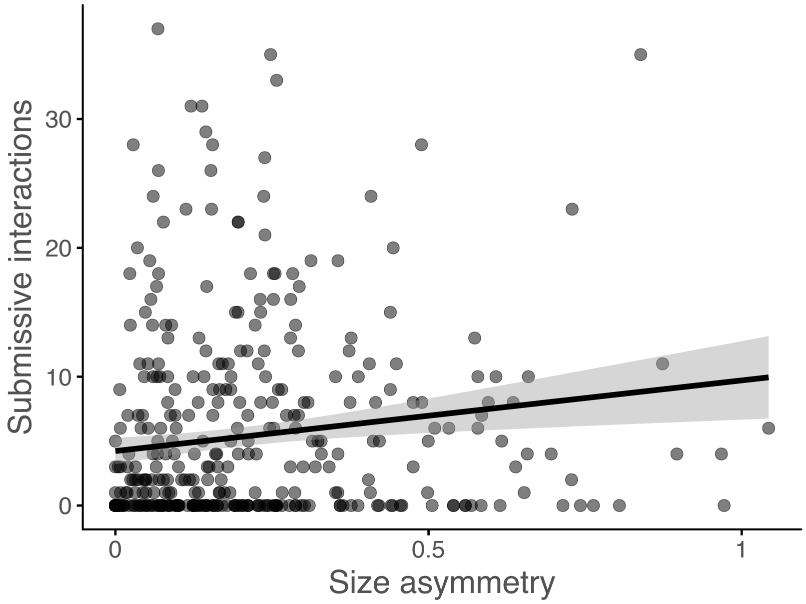
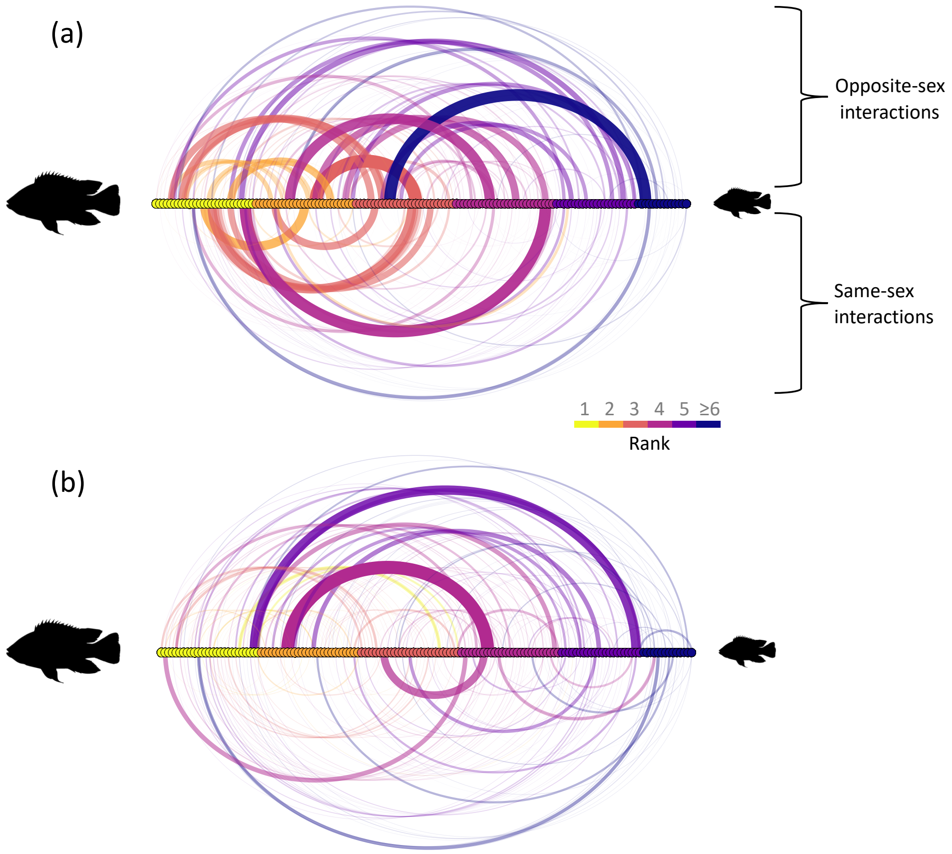


Figure 5


(a)
Opposite-sex interactions
Same-sex interactions
1 2 3 4 5 ≥6
Rank
(b)