

1 Subordinate submissive responses are predicted by dominant behaviour in a cooperatively breeding fish

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10

11 **Abstract**

12 In complex social groups, animals rely on communication to facilitate priority access to resources and
13 minimise the costs of conflict. Animals typically have more aggression signals than submission signals.
14 However, some social species do show multiple submission signals, and the context in which these different
15 signals are used is often not well understood. In the current study, we assessed agonistic interactions within
16 groups of the cooperatively breeding daffodil cichlid fish (*Neolamprologus pulcher*) to investigate the
17 relationship between the aggressive behaviours of the dominant breeding pair, and the submissive responses
18 of the highest ranked subordinate within the group. Daffodil cichlids may respond to aggression by fleeing or
19 by the production of either a tail quiver display or a head up display. Among the two submission signals, the
20 tail quiver display was used more frequently in response to a threat display while head up displays were
21 produced approximately equally in response to both threat displays and overt aggression. An exaggerated
22 version of the head up display was given more often in response to overt aggressions, suggesting a graded
23 submissive response both within and between the two submission signals. Within fish, the frequency of head
24 up displays, but not tail quiver displays, correlated positively with the frequency of threat displays received.
25 The current study helps us to better understand the use of submission signals in a highly social vertebrate
26 and sheds light on submission as an understudied aspect of communication.

27

28 Keywords: aggression; communication; daffodil cichlid; *Neolamprologus pulcher*; signalling; submission

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31 **1. Introduction**

32 Conflict is costly, and costs may not differ substantially between the winner and loser of an interaction, with
33 energetic expenditure, stress induced physiological responses, and the risk of injury or death, not differing
34 between competitors (Huntingford et al., 1987; Morrell et al., 2005; Hardy & Briffa, 2013). Conflict may also
35 lead to secondary costs, such as reduced vigilance, while increasing the risk of attracting predators (Jakobsson
36 et al., 1995). As a result, animals have evolved strategies to mitigate the costs of conflict (Briffa & Sneddon,
37 2010). For example, threat displays, opponent assessment, avoidance, and submission may help to minimise
38 costs (Archer, 1988; Hardy & Briffa, 2013; Briffa, 2014). Signals that reliably convey information about
39 aggressive motivation and fighting ability have evolved to benefit both the sender and the receiver of the
40 signal (Smith and Harper, 2003). Aggressive signals usually involve displays that emphasise traits relevant to
41 fighting ability, such as physical strength, size, and weaponry (Huntingford et al., 1987). Conversely, signals
42 that convey submission, typically deemphasise these traits (Bernstein, 1981; Reddon et al., 2022).

43 Submission signals are less well characterised in the literature than are aggression or dominance
44 signals, despite being widespread (e.g., Fox & Cohen, 1977; O'Connor et al., 1999; Ligon, 2014; Ruberto et
45 al., 2020). Most species have fewer submission signals than aggression signals (Bradbury & Vehrencamp,
46 1998). Although submission signals may be repeated or intensified (Eaton & Sloman, 2011) to ensure the
47 signal is successfully transmitted, multiple distinct submission signals which indicate varying levels of
48 submissive intent are uncommon, as a receiver may be less likely to accept a partial gesture of submission
49 (Matsumura & Hayden, 2006).

50 Agonistic communication is important for animals that live in groups. Group living is beneficial to the
51 members of the group (Hamilton, 1971; Roberts, 1996; Lehtonen & Jaatinen, 2016). However living in
52 proximity can increase the likelihood of conflict, which may offset these advantages, and thus conflict within
53 groups must be managed for group living to be a stable strategy (Lorenz, 1966; King, 1973; Krause & Ruxton,
54 2002). In social groups, the opportunity to flee from an attack may also be reduced by ecological or social
55 constraints (Matsumura & Hayden, 2006; Wong, 2010; Reddon et al., 2022), and therefore social stability
56 relies on effective communication (Frommen, 2020).

57 The daffodil cichlid (*Neolamprologus pulcher*) is a cooperatively breeding freshwater fish endemic to
58 Lake Tanganyika, East Africa (Taborsky & Limberger, 1981; Balshine et al., 1998). In the wild, daffodil cichlids
59 form stable groups, typically of 3-20 individuals, organised into linear dominance hierarchies based on body
60 size, which correlates with age (Balshine et al., 2001; Dey et al., 2013). The largest male and largest female
61 form a breeding pair who are socially dominant and engage in most of the reproduction in the group.
62 Dominant fish may be replaced due to predation events or territory takeovers, and larger subordinates
63 occasionally disperse between groups (Stiver et al. 2004). Subordinate group members assist the dominant
64 pair in raising their offspring and in defending the territory from predators and competitors (Wong &
65 Balshine, 2011). Within-group agonism is frequent and can result from disputes over status, workload, and
66 resource access (Wong & Balshine, 2011; Fischer et al., 2014; Hick et al., 2014; Balshine et al., 2017).
67 Dominant status is reinforced through threat displays and overt aggression (Dey et al., 2013; Balzarini et al.,
68 2017). Subordinates often flee from dominant aggression by swimming away rapidly (Balshine et al., 2017),
69 however, the ability to flee from aggression may be constrained by the danger of predation outside of the
70 group's territory (Groenewoud et al., 2016) and by the availability of shelters to flee to inside the territory
71 (Reddon et al., 2019). Subordinates may also signal submission through one of two displays: the head up
72 display (HUD; Table 1), or the tail quiver display (TQD; Table 1). Tail quiver displays are given in a variety of
73 social contexts including affiliation and courtship (Pisanski et al., 2015), as well as submission (Bayani et al.,
74 2017; Naef & Taborsky, 2020; Antunes et al., 2022). Head up displays by contrast seem to be used primarily
75 as a submission signal (Ruberto et al., 2020). The HUD may vary in intensity from a slight upwards tilt to the
76 adoption of a near vertical posture in the water column (Sopinka et al., 2009). The cause of this variation in
77 signal expression is unknown, it may be exaggerated to ensure signal transmission in more challenging
78 signalling environments such as the low visibility that occurs seasonally in Lake Tanganyika, or may represent
79 quantitative variation in submissive motivation, though the latter is not predicted by a model of submission
80 signalling (Matsumura & Hayden, 2006). Head up and tail quiver displays may occur in isolation or together,
81 either sequentially or simultaneously. Previous studies have often focused on one signal or the other (TQD:
82 (Bayani et al., 2017; Naef & Taborsky, 2020; Antunes et al., 2022); HUD: (Reddon et al., 2012; Hick et al.,
83 2014; Ruberto et al., 2020) or combined the two displays into a general submissive display category (Taves

et al., 2009). These two different displays may be used in different contexts or may depend on the level of submissive motivation.

In this study, daffodil cichlids belonging to 19 different social groups were observed under standardised environmental conditions. The relationships between aggressive behaviours of the dominant breeding pair, and the submissive responses of the largest subordinate in the group were recorded to examine what predicts the response of the focal subordinate fish. Specifically, how submissive responses varied based on the escalation level of the instigating aggression (threat display or overt aggression). We predicted that the TQD would mostly be used in response to less escalated threat displays, whereas HUDs and fleeing responses would be more frequent in response to overt aggression.

2. Methods

2.1 Study subjects and housing conditions

The research subjects were laboratory reared daffodil cichlids, *Neolamprologus pulcher*, which were descendants (F5-F7) of fish captured on the southern shore of Lake Tanganyika, Africa. Prior to the experiment, all fish were kept in mixed-sex groups of approximately 50 fish per aquarium (105 × 43 × 40cm, 180-litre). The housing tanks were equipped with a heater, a thermometer, two powered filters, an air stone, and 3 cm of fine coral sand. Temperature was maintained at 27 ± 1 C on a 12:12 h light:dark cycle with 15 min of gradual transition in lighting simulating sunrise and sunset. Fish were fed daily with a variety of dried prepared cichlid foods.

The study subjects were later moved into social groups (n = 19) housed in 90L aquaria (53 × 43 × 38 cm), each equipped with two foam filters, a heater, and a thermometer, along with 3 cm of fine coral sand. Each aquarium was furnished with 4 terracotta caves, used by the fish as breeding substrate as well as shelter, and two floating translucent green PET bottles, providing additional refuge. All animals were kept under the same husbandry regime previously described. Fish were housed in either small groups (n = 9), comprised of two dominant individuals and two subordinates, or larger groups (n = 10), which included the two dominant fish and 6-7 subordinates. Sex was only determined in the dominant pair, as many of the subordinates were

110 too small to be sexed by examination of the genital papillae. For each group, the sizes of the dominant
111 breeding pair and of the largest subordinate were recorded, by measuring the standard length of each fish
112 from the tip of the snout to the end of the caudal peduncle (standard length mean \pm SD: dominant male =
113 5.25 \pm 0.48cm; dominant female = 4.75 \pm 0.52cm; focal subordinate = 3.5 \pm 0.45cm). We aimed for
114 approximately a 5-10% difference in body size between breeders, and between adjacent subordinate ranks,
115 with size difference of approximately 25-35% difference between breeder female and largest subordinate,
116 mimicking the size distribution of wild groups. Subordinate individuals were moved into the experimental
117 tanks 24 h before the dominant pair. Groups were housed together for at least one month prior to
118 observation to allow for groups to stabilise while reducing variation across the observation period due to
119 uncertainties in the hierarchy. On the rare occasions that members were rejected during group formation,
120 groups were dissolved and new ones were formed using new fish from the stock aquaria.

121

122 **2.2 Video recordings**

123 The 19 groups were recorded with a camera (CX240E Full HD Camcorder, Sony Corp., Japan), from a frontal
124 perspective capturing the entire aquarium. Each group was recorded four times over a period of two weeks
125 between 10:00-15:00, with only one recording captured per day. Each recording was 30 minutes long, leading
126 to a total of 120-minutes of recording per group. The first 10 minutes of each recording were treated as a
127 habituation period and were therefore not coded, resulting in 80 total minutes of coded observation per
128 group, which were summed together for analysis purposes.

129

130 **2.3 Behavioural coding**

131 We recorded each instance of aggression from either member of the dominant pair towards the largest
132 subordinate (focal fish) and the focal fish's response to that aggression (see Table 1 for a detailed description
133 of the coded behaviours). For each agonistic interaction (n = 369) we recorded the sex of the aggressor and
134 whether they performed an overt aggression or a threat display. The subordinate response was recorded for
135 each interaction as either a submission display (HUD or TQD) or a flee. Moreover, if the submission display
136 was a HUD, the angle of the tilt was visually estimated as being above or below 45° relative to the substrate

137 by pausing the video at the apex of the display. HUD and TQD were recorded as separate responses when
 138 they were carried out sequentially or simultaneously in response to a single aggressive act.

139

140 **Table 1.** Ethogram of agonistic behaviour for the daffodil cichlid, *Neolamprologus pulcher*.

141

TYPE OF INTERACTION	BEHAVIOUR	DESCRIPTION
<i>Overt aggression</i>	Chase	The dominant fish swims rapidly towards the subordinate for a distance of at least 4 cm.
	Bite/ram	The dominant fish makes contact between their mouth and the body of the subordinate
<i>Threat displays</i>	Aggressive posture	The dominant fish faces the subordinate with their head lowered, tail raised upwards, and fins extended.
	Opercular threat	The dominant fish swims towards the subordinate with its jaws open and opercula extended outward. The pectoral fins are spread, while the body is tilted slightly downwards.
<i>Submission (display)</i>	Head up display (HUD)	The subordinate fish responds to an aggression by tilting their body upwards and exposing their ventral aspect to the receiver.
	Tail quiver display (TQD)	The subordinate fish responds to aggression by producing a bilateral oscillation of the tail. Motion originates at the tail and can extend to the entire body.
<i>Submission (escape)</i>	Flee	The subordinate fish responds to aggression by quickly swimming away, for a distance of at least 4 cm.

142

143

144 2.4 Data analysis

145 To examine the effect of the type of inciting aggression on the type of submissive behaviour elicited, we fit a
 146 generalised linear mixed model to a multinomial logistic distribution. Dominant aggression was coded
 147 categorically as an overt aggression or a threat display and included as a predictor variable. Although not the
 148 focus of this study, we also included the group size (small, large) and the sex of the aggressor (male, female)

149 as predictor variables as the broader social context could affect the submissive responses observed. The
150 behavioural response from the focal fish was coded categorically as a HUD, a TQD, or a flee and included as
151 the response measure. Focal identity was included as a random factor to account for multiple interactions
152 per focal individual contributing to the dataset.

153 In a follow-up analysis, we compared only the subordinate submission signals (HUD, TQD) depending
154 on the dominant behaviour (overt aggression, threat display), the sex of the dominant and the size of the
155 group, using a generalised linear mixed model fit to a binomial logistic distribution. Group size and dominant
156 sex were included as fixed factors and focal identity was included as a random factor.

157 The frequencies of HUDs above or below an angle of 45° in response to overt aggression or threat
158 displays were examined with a generalised linear mixed model fit to a binomial logistic distribution. Type of
159 aggressive behaviour received, the size of the group, and the sex of the aggressor were included as predictor
160 variables. The response variable was the angle of the HUD relative to the substrate, coded categorically as
161 HUD $>45^\circ$ or HUD $<45^\circ$. The identity of the focal fish was included as a random factor. For all models, fixed
162 effects were tested with Wald F tests.

163 We examined the Pearson product-moment correlation between the number of threat displays or
164 the number of overt aggressions that the focal fish received from the dominant pair with the number of HUDs
165 or TQDs they showed in response ($n = 19$). Data analysis and visualisation were conducted using SPSS (v. 27)
166 and R (v. 3.6.2).

167

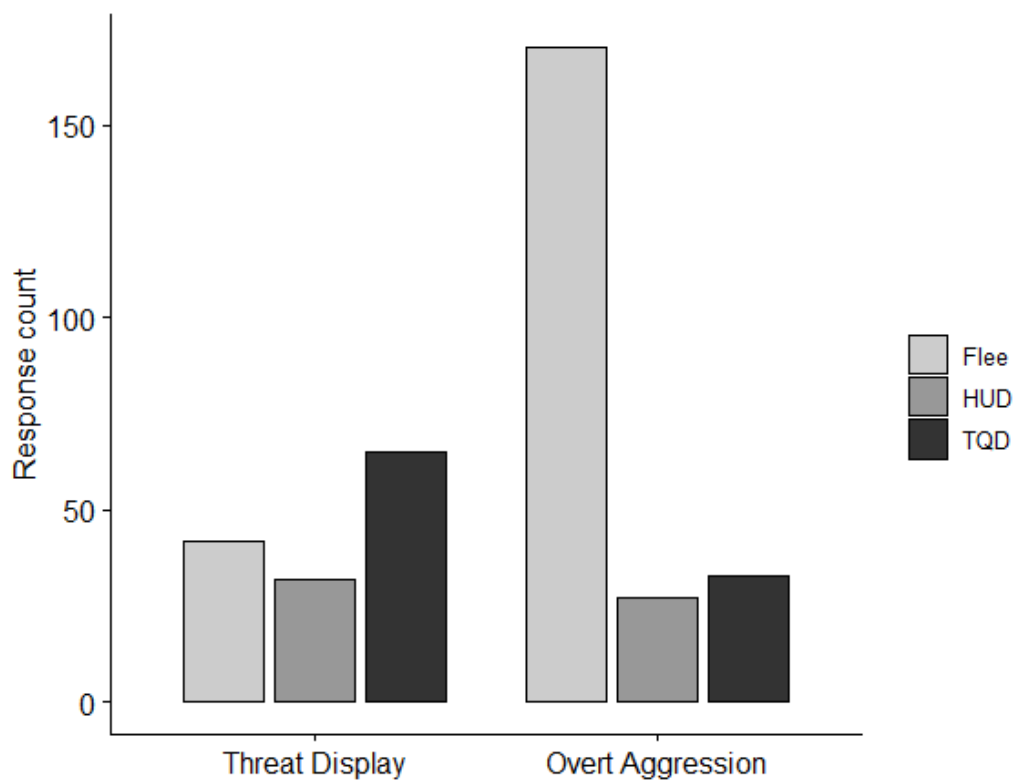
168 **2.5 Ethical statement**

169 Animal housing and handling protocols were approved by the Liverpool John Moores Animal Welfare and
170 Ethics Steering Group (approval number: AR_TR/2018-4) and adhered to the guidelines of the Animal
171 Behaviour Society and the Association for the Study of Animal Behaviour.

172

173 **3. Results**

174 The type of aggression shown by the dominant fish (overt aggression or threat display) significantly predicted
 175 the submissive response of the focal fish ($F_{2,361} = 27.69$, $p < 0.001$, Fig. 1) with flees being much more common
 176 in response to overt aggression and TQD being more likely in response to threat displays. Neither group size
 177 nor the sex of the aggressor had a significant effect on the focal response (Group size: $F_{2,361}=1.89$, $p = 0.15$;
 178 Sex: $F_{2,361}=1.18$, $p = 0.31$).
 179



180
 181 **Figure 1.** Counts of submissive behaviour in the largest subordinate in response to dominant aggression in
 182 80 minutes of observation. The type of submissive response depended on the type of aggression received
 183 ($p < 0.001$).

184 Restricting the analysis to only submission display responses (i.e., excluding those interactions in
 185 which the focal fish fled from the dominant aggression), there was no significant effect of aggression type
 186 ($F_{1,153} = 1.49$, $p = 0.22$), dominant sex ($F_{1,153} = 0.03$, $p = 0.86$), nor group size ($F_{1,153} = 0.09$, $p = 0.76$), on the
 187 likelihood of the focal fish producing a TQD compared to a HUD in response to dominant aggression.

188 Aggression type received significantly predicted the likelihood of a HUD being greater than 45°
 189 ($F_{1,54}=5.68$, $p=0.021$; Fig. 2), while group size ($F_{1,54}=0.23$, $p=0.64$) and sex ($F_{1,54}=0.04$, $p=0.84$) did not.

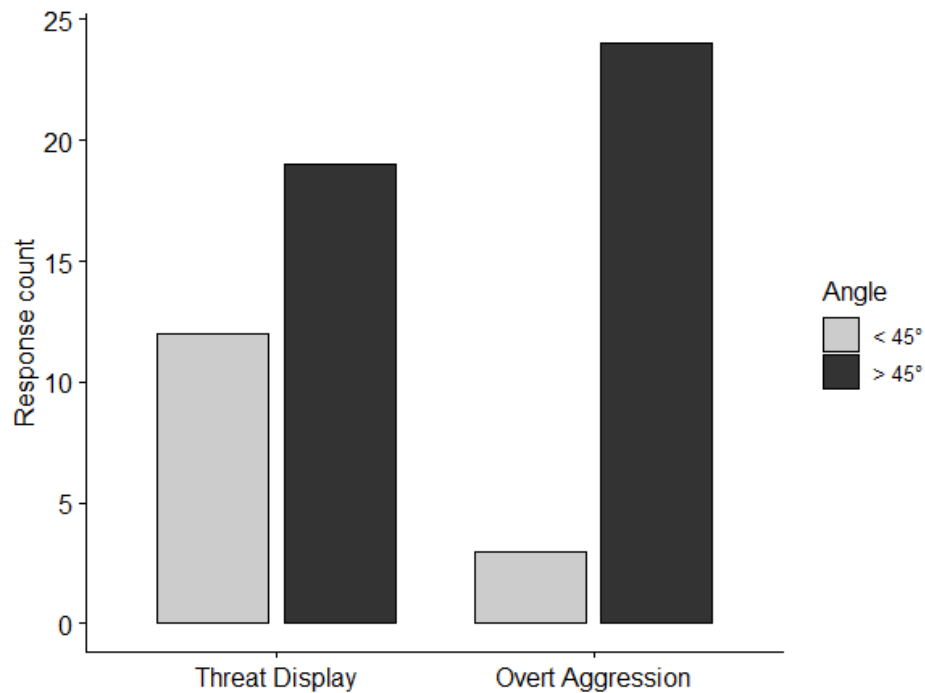


Figure 2. Counts of HUDs elicited above or below 45° relative to the substrate in response to dominant aggression in 80 minutes of observation. The tendency for the HUD to involve a greater tilt of the body was predicted by dominant behaviour ($p = 0.02$).

There was a significant positive relationship between the number of threat displays from the dominant fish and the number of the HUDs shown by the focal subordinate ($r = 0.65$, $N = 19$, $p = 0.002$, Fig. 3A). In contrast the number of TQDs shown by the focal fish was not significantly predicted by the number of threat displays received ($r = 0.27$, $p = 0.26$, $N = 19$, Fig. 3C). The number of overt aggressions from the dominant pair was not significantly related to the number of HUD shown ($r = 0.40$, $N = 19$, $p = 0.09$, Fig 3B) or the TQD shown by the focal fish ($r = -0.11$, $N = 19$, $p = 0.67$, Fig. 3D).

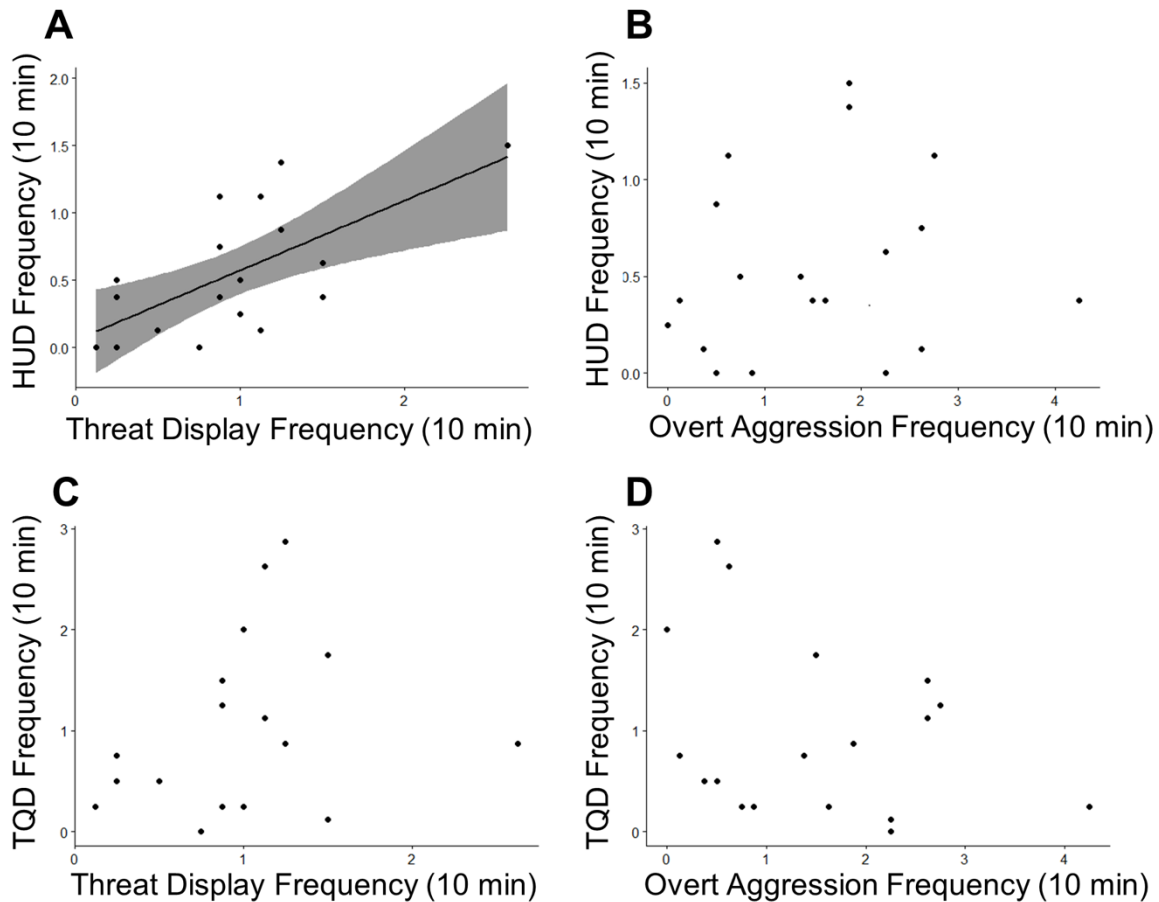


Figure 3. The linear relationship between the aggression received from the dominant fish and the number of submission displays shown by the focal subordinate per 10 minutes of observation. (A) There is a significant positive relationship between the number of threat displays received and the number of HUD shown ($p = 0.002$). (B) The number of overt aggressions was not significantly related to the number of HUD ($p = 0.09$). Neither (C) threat displays ($p = 0.26$) nor (D) overt aggressions ($p = 0.67$) received from the dominant pair significantly predicted the number of TQD by the focal fish. Linear best fit lines for significant relationships are shown with 95% CI.

4. Discussion

Using detailed observations of 19 laboratory housed groups of daffodil cichlids (*Neolamprologus pulcher*), we found that the escalation level of the aggression shown by the dominant breeding pair towards their largest subordinate helper strongly predicted the resultant submissive response. When one of the dominant pair attacked the focal subordinate by chasing or biting, the subordinate most often fled from the interaction.

228 When the dominant showed a threat display, the focal fish was more likely to show a submission display in
229 response. Both head up displays (HUD) and tail quiver displays (TQD), were produced in response to both
230 overt aggression and threat displays from the dominant pair. The number of head up displays was predicted
231 by the number of threat displays received. By contrast, the TQD was not significantly associated with the
232 number of overt aggressions or threat displays received, suggesting the HUD may be a more specialised
233 submission display than the TQD. We also found that the HUD was more likely to be exaggerated through a
234 more dramatic tilt of the body axis when the inciting aggressive act was an overt aggression rather than a
235 threat display, suggesting possible gradation of submissive motivation within signal type.

236 Both the HUD and the TQD are used as submission signals in the daffodil cichlid, and the context in
237 which they are used overlaps substantially. Submission signals need to be effectively received by dominant
238 individuals to modulate their aggression (Reddon et al., 2022), and daffodil cichlids could use graded or
239 differentiated displays to ensure that signals are efficiently transmitted and received across signalling
240 contexts. For example, brown trout (*Salmo trutta*) show submission by darkening their body colouration, and
241 do so more dramatically in turbid water, possibly to enhance signal transmission when visibility is reduced
242 (Eaton & Sloman, 2011).

243 Although submissive repertoires are generally not as diverse as aggressive repertoires (Bradbury &
244 Vehrencamp, 1998), examples of animals using more than one submission display are known. For example,
245 Jacky dragons (*Amphibolurus muricatus*) deploy two different submission displays (slow arm waves and slow
246 head bows) during opponent assessment (Carpenter et al., 1970; Van Dyk & Evans, 2008). In canids such as
247 dogs (*Canis l. familiaris*), wolves (*Canis lupus*) and African wild dogs (*Lycaon pictus*), subordinate group
248 members communicate submissive intentions through what is referred to as passive vs. active submission
249 (Schenkel, 1967; Cordoni & Palagi, 2008; Baan et al., 2014; Van den Berghe et al., 2019). These passive and
250 active displays can take place separately or in combination. Both displays involve crouched posture and
251 lowered tail and ears, but these are performed more dramatically in passive displays (Schenkel, 1967). Both
252 displays convey submission, but active displays may also signal affiliative motivation (e.g., during greeting
253 ceremonies), while passive displays are given primarily in response to dominant inquisitive behaviours (e.g.,
254 sniffing urogenital areas) or aggression (Schenkel, 1967). Even greater complexity in signal repertoire is

255 observed in social primates such as ring-tailed lemurs (*Lemur catta*). This species' visual and acoustic
256 repertoire includes several submissive postures (Pereira & Kappeler, 1997) and vocalisations (Macedonia,
257 1993). Interestingly, vocal signals are elicited in context dependent agonistic interactions, with yips, cackles
258 and twitters given by submissive individuals when losing agonistic interactions, and chutters elicited by both
259 winners and losers (Bolt, 2021), supporting the existence of intricate signalling systems to mitigate conflict.

260 As with the canid and primate examples, the relatively rich submissive repertoire of daffodil cichlids
261 could be explained by the social complexity hypothesis for communicative complexity. Socially complex
262 environments can promote the evolution of social cognition, which in turn favours the greater nuance in
263 communication necessary to support behavioural coordination (Freeberg et al., 2012; Sewall, 2015).
264 Cooperative breeding systems are commonly affected by high levels of intra-group social conflict, and the
265 evolution of multiple submission signals in daffodil cichlids could fulfil the need for social context-dependent
266 communication. Alternatively, cooperation per se may not necessarily lead to richer submissive repertoires,
267 but rather may increase the frequency of submission signals and/or reduce the threshold at which they are
268 elicited (Reddon et al., 2022). Recent studies testing these predictions in birds have produced conflicting
269 results (Rosa et al., 2016; Leighton, 2017), highlighting the current lack of agreement surrounding signal
270 evolution in cooperative systems. According to previous analyses comparing cooperative and non-
271 cooperative cichlids, communication repertoires appear to be similarly structured in close relatives across
272 social systems (Hick et al., 2014; Balshine et al., 2017). Furthermore, social complexity should be enhanced
273 when multiple individuals interact, due to eavesdropping and audience effects (Valone, 2007; Zuberbühler,
274 2008). In the current study however, group size did not affect submission responses, suggesting that
275 eavesdroppers and rank conflict elsewhere in the hierarchy may not have a major effect. Breeder sex also
276 did not affect the subordinate response, but it should be noted that the sex of the subordinate was unknown,
277 as many individuals were too small to be visually sexed. This lack of information may have obscured sex
278 specific patterns, as aggression from the dominant breeders could depend on whether they are interacting
279 with same versus opposite sex group mates.

280 The observed overlap between the HUD and TQD may be the result of these signals fulfilling subtly
281 distinct, context-dependent functions. Both signals were elicited in response to dominant aggression, but the

282 HUD was more strongly correlated with threat displays. We recently reported that individuals performing
283 more HUDs receive less aggression from dominant fish (Ruberto et al., 2020). Our current findings seem to
284 indicate that HUDs may be a more specific social signal in daffodil cichlids, serving to de-escalate the
285 dominant aggressive interactions. Moreover, it is possible that differences in the angle of the body tilt in the
286 HUD indicates gradation of submissive motivation in the subordinate fish, allowing the HUD to act as a
287 nuanced submission signal.

288 The TQD occurred at higher rates in comparison to the HUD but in contrast, it wasn't significantly
289 correlated with aggression received. This display may be co-opted from other communicative contexts to
290 serve as a submissive-affiliative signal: the TQD is often observed during courtship, and it is conserved across
291 a diverse array of cichlids in this context (Baerends & Baerends-van Roon, 1950; Barlow, 2008), while the
292 HUD appears to be more species-specific. It is possible that subordinate cichlids use the TQD as a
293 multipurpose affiliative-submissive signal, indicating both subordination and affiliation to higher ranked
294 individuals, while the HUD is more strictly used to show immediate submission in response to acute
295 aggression. In other animal species submission signals are reported to serve a multipurpose submissive-
296 affiliative function, as in the case of wolves (Schenkel, 1967; Cafazzo et al., 2010). Displays can be
297 differentiated when used to either de-escalate aggression or to pre-emptively appease the dominant
298 individual, in what are sometimes referred to as submission signals (the former) or subordination (the latter;
299 (Preuschoft & van Schaik, 2000). In wolves, submission signals, such as back rolling, are usually given as an
300 immediate behavioural response following a dominant physical attack, particularly when avoidance
301 behaviours or escape are not a viable option (van Hooff & Wensing, 1987). Subordination signals are primarily
302 directed at dominants outside of the agonistic context, reinforcing subordinate status (van Hooff & Wensing,
303 1987). Dominant individuals are often approached and greeted by subordinates with stereotypical lowered
304 posture, followed by lip licking and other appeasing behaviours to reemphasise status within an established
305 social relationship. The use of signals for both submission and subordination purposes is also reported in
306 other hierarchical species, such as Verreaux's sifakas (*Propithecus verreauxi*; (Flack & de Waal, 2007). Chatter
307 vocalisations are used both as immediate response to aggression, but also when aggressive provocation is

308 not apparent, to communicate peaceful intentions, and they are found to reduce within-group conflict while
309 promoting hierarchical stability through reconciliation (Lewis, 2019).

310 It is possible that the space limitation imposed by the aquarium environment may have affected the
311 conflict management strategies of daffodil cichlids, for example by making fleeing a less viable response, or
312 by increasing the frequency or intensity of aggression from the dominants. Although the behaviour of daffodil
313 cichlids is known to be broadly similar in the wild and in the laboratory (Taborsky & Grantner, 1998), we did
314 find a higher rate of aggression in our observations than has previously been seen in the field (an average of
315 2 aggressions per 10 minutes in our sample vs. 0.4 per 10 minutes in the field; Hellmann et al., 2015). Some
316 of this difference may be explained by the difficulty of recording behaviour in the field vs. laboratory setting,
317 with more instances of aggression likely to be missed while observing live via SCUBA compared to coding
318 from high-definition video. It should be noted that space limitations are also present in the wild as this species
319 is highly territorial, defends a relatively small territory ($\sim 1\text{m}^3$), and is exposed to extreme predation threat
320 when venturing outside (Groenewoud et al., 2016). It is possible that subordinates in the wild may make
321 greater use of shelters that are too small to be accessed by the dominants due to the difference in the body
322 size, whereas all shelters were large enough to be used by all fish in our laboratory setup. Future work should
323 examine the importance of shelter size and space limitation on conflict management in daffodil cichlids.

324 In conclusion, we found that dominant aggressive behaviour was a strong predictor of subordinate
325 submissive responses in the cooperatively breeding daffodil cichlid. The most common response to an overt
326 aggression was to flee, while submission signals were more common in response to a threat display. Both
327 the HUD, and the TQD were used in response to both threat displays and overt aggression. However, the
328 number of HUD shown was predicted by the number of threats received, while the angle of HUD varied with
329 the type of aggressive behaviour received. These results suggest that the HUD is being used more specifically
330 as a nuanced submission signal, while the TQD may have other social functions. We found evidence to suggest
331 that daffodil cichlid subordinates communicate variation in submissive motivation with both multiple
332 submission signals and variation in the expression of those signals. It is possible that socially complex groups
333 may select for greater nuance in submission signalling than would be expected in one-off interactions.

334

335 Acknowledgements

336 Thanks to Chelsie Hirons-Major for comments on an earlier version of the manuscript. This work was
337 supported by a Royal Society Research Grant (RGS1191237) to AR. TR was supported by a Liverpool John
338 Moores University Faculty of Science PhD Studentship.

339

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