Head up displays are a submission signal in the group-living daffodil cichlid

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ABSTRACT

Dominance hierarchies can reduce conflict within social groups and agonistic signals can help to establish and maintain these hierarchies. Behaviours produced by subordinates in response to aggression are often assumed to function as signals of submission, however, these behaviours may serve other purposes, for example, defence or escape. For a behaviour to act as a submission signal, the receiver must respond by reducing their likelihood of further aggression towards the signaller. In the current study, we examine the receiver response to a putative signal of submission, the head up display, within established social groups of the cooperatively breeding fish, the daffodil cichlid (*Neolamprologus pulcher*). We found that when subordinate signallers produce the head up display in response to aggression from the breeder male, he exhibited a longer latency to behave aggressively towards that individual again. We also report that head up displays are rarely produced without being elicited by aggression, and the number of head up displays correlates with the amount of aggression received. Our results demonstrate that the head up display is used as a signal of submission in the daffodil cichlid and provide insight into intragroup communication in an emerging model system for the study of social behaviour.

Keywords: aggression, communication, cooperative breeding, fish, *Neolamprologus pulcher*, submissive

1. Introduction

Group living confers many benefits to those within the group, including but not limited to increased safety from predators (Alexander, 1974; Krause & Ruxton, 2002). Yet, within group conflict may impose sufficient costs on some group members (King, 1973; Krause & Ruxton, 2002; Lorenz, 1963) to destabilise social groups or prevent the formation of groups to begin with (Aureli, Cords, & Van Schaik, 2002; de Waal, 1986; Kutsukake & Clutton-Brock, 2008; Silk, 2007). Adaptations that mitigate conflict within social groups are a universal feature of animals living in complex social groupings (Aureli & de Waal, 2000). In this context, dominance hierarchies can help to avoid conflict within established social groups by setting priority access to resources without the need for frequent costly aggressive interactions (Bernstein, 1981; Drews, 1993; Rowell, 1974; Wilson, 2000). In order to establish and maintain dominance hierarchies, animals make use of both stable markers of social status, for example differences in colouration or markings (Cervo, Dapporto, Beani, Strassmann, & Turillazzi, 2008; Chen & Fernald, 2011; Dey, Dale, & Quinn, 2014), and more flexible behavioural indicators of status (Ward & Webster, 2016), with or without individual recognition mechanisms (Dugatkin & Earley, 2004). Signals of agonistic intent help to stabilise dominance hierarchies, and therefore promote group living (Bernstein 1981, Frommen 2020). Submission signals in particular allow subordinate individuals to communicate their lack of motivation to perpetuate or escalate an aggressive interaction against a socially dominant and/or physically superior receiver (Bernstein, 1981; Deag & Scott, 1999; Flack & de Waal, 2007; Petit, 2010). As a result, submission signals are an essential aspect of communication within complex social groups (Bernstein, 1981; Freeberg, Dunbar, & Ord, 2012; Frommen, 2020; Schenkel, 1967), and are widespread throughout the animal kingdom (Balshine, Wong, & Reddon, 2017; Judge

& de Waal, 1993; Reddon, Dey, & Balshine, 2019; Sánchez-Hernández, Ramírez-Pinilla, & Molina-Borja, 2012).

To act as a signal of submission, a behaviour must reduce the likelihood of further aggression from the receiver (Bradbury & Vehrencamp 1998). For example, in contests between veiled chameleons (*Chamaeleo calyptratus*), the losing individual signals their lack of intention to persist by darkening their body colouration. The receiver reacts to this darkening of the body with a precipitous decrease in further aggression (Ligon, 2014). Similarly, several fish species change their body colouration in response to aggression: for instance, the common blenny (*Lipophrys pholis*) blanch to signal submission, thereby reducing aggression received (Gibson, 1967). Oscars (*Astronotus ocellatus*) defeated in a contest change their body patterns into a uniform dark colouration (Beeching, 1995), while salmon (*Salmo salar*) darken their body and eye colour to indicate submission (O'Connor, Metcalfe, & Taylor, 1999), and in both cases this darkening reduces aggression from the receiver. Signallers may use vocalisations or assume a non-threatening body posture, for example by lowering their ears and tail (Fox, 1969; Leyhausen & Tonkin, 1979) to communicate their submission towards an aggressive individual. In fallow deer (*Dama dama*), the lateral display of the antlers, turning the head away from an opponent by the loser of a contest serves to de-escalate the conflict (Jennings, Gammell, Carlin, & Hayden, 2002). Similarly, in little blue penguins (*Eudyptula minor*), turning the head to look away from an attacker is used as a submission signal (Waas, 1990).

However, not all ostensibly submissive behaviours may actually decrease the aggressiveness of the receiver, at least not in all contexts in which the behaviour is produced. In the case of meerkats (*Suricata suricatta*), overly subordinate females receive more aggression from the dominant pair and are most likely to be evicted from the social group, compared to less deferential individuals (Kutsukake & Clutton-Brock, 2008). On the other hand, seemingly submissive behaviours may be used by animals as a defensive tactic during contests to protect a vulnerable part of their body, or even as a way to prepare a counterattack (Pellis & Pellis, 2015). For example, rolling over on to the back and assuming a supine posture, which is a frequent manoeuvre during play fights (Bauer & Smuts, 2007; Fox, 1969), also has an apparent submissive function in dogs and wolves (Lorenz, 1943; Schenkel, 1967). However, in both dogs (Norman, Pellis, Barrett, & Henzi, 2015) and wolves (Cordoni, 2009), this behaviour has been found to be more consistently used as a combat tactic than as a submission signal. Similarly, jacky dragons (*Amphibolurus muricatus*) were found to strategically use the same signals to escalate or de-escalate a conflict, depending on the context of the signals produced by their opponent (Van Dyk & Evans, 2008).

The cooperatively breeding cichlid fish *Neolamprologus pulcher*, commonly known as the daffodil cichlid, is a freshwater species endemic to Lake Tanganyika, Africa (Balshine, Neat, Reid, & Taborsky, 1998; M. Taborsky & Limberger, 1981). These small fish form permanent social groups organised into a size-based dominance hierarchy (Wong & Balshine, 2011). A group of daffodil cichlids is generally composed of a dominant pair, usually the largest male and female fish, and 1-20 smaller subordinate fish of varying size (Balshine et al., 2001; Desjardins, Fitzpatrick, Stiver, Van der Kraak, & Balshine, 2008; Heg, Brouwer, Bachar, & Taborsky, 2005; M. Taborsky, 1984, 1985). In daffodil cichlid groups, only the dominant pair typically reproduce, while both breeders and subordinates work together to guard and maintain the territory, and take care of the offspring (Wong & Balshine, 2011). Conflicts and agonistic behaviours among group members are well-documented in this species (Balshine et al., 2017; Reddon, Balk, & Balshine, 2013; Reddon et al., 2011). Potential sources of conflict within *N. pulcher* social groups include the availability of suitable shelters (Hick, Reddon, O'Connor, & Balshine, 2014; Reddon et al., 2011) and the distribution of workload among group members (Fischer, Zöttl, Groenewoud, & Taborsky, 2014). The proximity of subordinate individuals to breeding positions is also known to generate competition (Dey et al. 2013), and changes in the hierarchy of a social group may induce aggressiveness in individuals ascending in rank as a way to re-establish dominance relationships (Wong & Balshine, 2010).

Previous empirical and theoretical work has established that movement restrictions correlate with the expression of submission signals (Aureli & de Waal, 2000; Huntingford & Turner, 2013; Matsumura & Hayden, 2006; Schenkel, 1967). Submission is more common when the subordinate animal is unable to easily move away from or escape aggression from the dominant individual, for instance, in chameleons, because of their low movement speed (Ligon, 2014). Daffodil cichlids are highly capable swimmers; however, their movements are restricted by their environment. Daffodil cichlids are reliant upon their continued membership within the social group for survival due to the high predation pressure (Groenewoud et al., 2016). So, while daffodil cichlids could escape aggression from a higher ranking group member in the wild, to do so might necessitate leaving the small, sheltered, territory protected by the group and thus risk being depredated (Balshine et al., 2001; Groenewoud et al., 2016; Wong & Balshine, 2011). Hence, there is good reason to assume that submission signals ought to be an important aspect of the social repertoire of this species (Balshine et al., 2017; Reddon et al., 2019). Submissive behaviours may prevent aggression from higher ranking group members (Bergmüller & Taborsky, 2005; Fischer, Bohn, Oberhummer, Nyman, & Taborsky, 2017; Fischer et al., 2014), and increase the likelihood that a subordinate may be accepted as part of the group (B. Taborsky, Arnold, Junker, & Tschopp, 2012). Thus, they are likely an important factor in cementing the social groups (Balshine et al., 2017; Fischer et al., 2017; M. Taborsky & Grantner, 1998).

Subordinate daffodil cichlids frequently perform a behaviour known as the head up display (HUD) in which the fish tilts its body upwards in the water column, revealing its underbelly to another fish (Hick et al., 2014). The HUD may be accompanied by a quivering of the tail, or even of the entire body (Hick et al., 2014). Subordinates often respond to aggression from more dominant fish with HUDs, suggesting this behaviour may serve as a submission signal (Balshine et al., 2017; Bergmüller & Taborsky, 2005; Reddon et al., 2019). However, it remains unknown if receiving the HUD actually reduces the likelihood of future aggression.

In the current study, we aimed to confirm that the HUD in the daffodil cichlid does indeed serve as a submission signal within social groups. We predicted that the receiver would reduce the frequency of further aggression by increasing the average latency to the next aggression directed at the signalling individual.

2. Methods

Study animals

The daffodil cichlids (*Neolamprologus pulcher*) used in this experiment were laboratory reared descendants of animals captured from Kasakalawe Bay along the southern shore of Lake Tanganyika (Zambia, Africa). Prior to the onset of the study, the subjects were housed in mixed sex stock aquaria (105 x 43cm and 40cm high, 180-litre) at a density of approximately 50 fish per aquarium. These stock aquaria contained 2 internal powered filters, a heater, a thermometer, an air stone, and 3cm of fine coral sand. The stock aquaria were held at 27±1°C on a 12:12h light:dark cycle, with 30 minutes of gradual brightening/dimming to simulate sunrise and sunset. The aquaria were regularly checked for water quality parameters. Fish were fed daily on cichlid flake food (Tetra Cichlid XL Flakes, Tetra Werke, Germany).

2.1. Focal groups

We created 9 focal social groups of 4 fish each by transferring fish from the stock aquaria into 90-litre (53 x 43cm and 38cm high) group housing aquaria. Each group consisted of a breeder male (mean ± SE standard length, measured from the tip of the snout to the end of the caudal peduncle = 5.33 ± 0.19cm), a breeder female (mean ± SE standard length = 4.80 ± 0.16), and two smaller subordinates of indeterminate sex. Of the two subordinates, the larger within each group was referred to as “subordinate 1” (mean ± SE standard length = 3.31 ± 0.19cm) and the smaller of the two as “subordinate 2” (mean ± SE standard length = 2.72 ± 0.11cm).

These groups were formed by first introducing the subordinates into the new aquarium, and then 24h later, adding the larger individuals. New groups were carefully monitored for the social rejection of any group members, and unstable groups were dissolved and reformed with new fish. All groups used in this study lived together as a group for at least one month prior to observation and had successfully produced offspring at least once. At the time of observation, all groups contained fry (<1cm standard length). Consistent with previous reports (Dey, Tan, O’Connor, Reddon, & Caldwell, 2015), we did not observe adult or larger juvenile daffodil cichlids interact with fry.

Each of the group housing aquaria was furnished with two foam filters, a heater, a thermometer, 3 cm of fine coral sand, along with 4 terracotta caves to serve as shelters and breeding substrate. Two additional floating shelters made from translucent green PET bottles were provided near the surface of the water to provide additional refuges for the subordinates. The husbandry regime for the social groups was identical to that of the stock housing aquaria.

2.2. Observations

Each group was recorded with a video camera (CX240E Full HD Camcorder, Sony Corp., Japan) from a front-on perspective for five 30-minute periods over the course of two weeks, resulting in a total of 150 minutes of observation per group. The video recordings were captured between 10h and 16h and only one recording was taken per day.

2.3. Coding

A trained observer (JT), blind to the study hypotheses, coded all of the videos. We focused on the interactions between the dominant breeder male and the other three group members (breeder female, subordinate 1, subordinate 2). The breeder male frequently showed aggression to other group members and never showed HUDs, consistent with previous reports (M. Taborsky & Grantner, 1998).

For each group, we recorded every instance of aggression directed by the breeder male to any of the other three group members. We recorded five different behaviours as aggression: chases, rams, bites, head down displays, and frontal displays (for a detailed description of these behaviours, see (Reddon et al., 2015)). We also recorded every instance of a HUD produced by any of the other three group members towards the breeder male. We defined the HUD as a body posture in which the head of the focal fish is pointed upwards in the water column (in some occasions the body may be held completely vertically) and its tail downwards (Hick et al., 2014).

Following each act of aggression from the breeder male towards one of the other three group members, we recorded whether or not the receiving fish responded with a HUD, and then recorded the latency (in seconds) to the next instance of aggression from the breeder male to that individual.

2.4. Statistical analysis

We used a Linear Mixed Model (LMM) to examine the relationship between the number of aggressive behaviours received from the breeder male and the number of HUDs directed at the breeder male. We included rank (breeder female, subordinate 1, subordinate 2), and the interaction between rank and aggression received as fixed effects. In a separate LMM, we examined the latency to the next aggression from the breeder male following a HUD compared to aggression that did not elicit a HUD in the focal fish. For this analysis, we included only fish for which we observed at least two instances of each type of response to breeder male aggression (HUD shown, HUD not shown). This reduced the sample size for this analysis to n = 17 focal fish, which included at least one focal fish from each social group. We calculated the mean latency to the next aggression from the breeder male after each type of response for each fish and treated response type as a repeated measure within each focal individual. We log10 transformed the mean latency to the next aggression prior to analysis to account for the positive skew in this data but present the raw data graphically. For both models, individual and social group were included as random factors. We checked all models for adherence to model assumptions by examining the Q-Q plots of the model residuals. All statistics were performed using SPSS version 26.0 (IBM) for Macintosh (macOS 10.15.4).

2.5. Ethical note

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

Each of the experimental group housing aquaria was furnished with 4 terracotta caves plus two additional floating shelters to act as refuges. New groups were carefully monitored for the rejection of any group members (i.e., constantly receiving aggression, always swimming close to the surface of the water, and seldom interacting with the rest of the group). Unstable groups were dissolved and returned to the stock aquaria, and then remade with new fish. All observations were drawn from stable social groups showing species typical levels of agonism (Balshine et al., 2017). All fish were carefully monitored during the study. If any fish had shown signs of social rejection, that group would have been dissolved and the fish returned to the stock aquaria. This was never required once stable groups had formed.

3. Results

Across the 27 focal fish in 9 groups, we recorded 493 instances of HUDs directed towards the breeder male who produced 611 instances of aggression towards the focal fish in 1350 total minutes of observation. The vast majority (94.5%) of HUDs directed towards the breeder male were performed in direct response to aggression.

There was a positive linear relationship between the aggression directed towards each focal fish by the breeder male and the number of HUDs performed to him by those fish ($F_{1,20.42} = 9.26$, $p = 0.006$; Fig. 1). There was no significant effect of rank ($F_{2,20.38} = 0.20$, $p = 0.82$) nor an interaction between rank and aggression received on the number of HUDs performed ($F_{2,20.44} = 1.37$, $p = 0.28$).

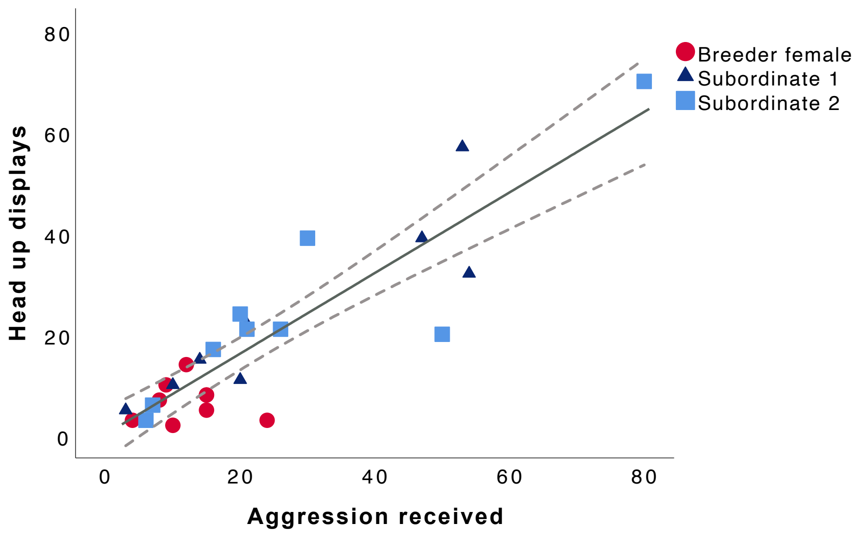

Figure 1. The number of head up displays directed at breeder males as a function of breeder male aggression towards each fish. There is a positive linear relationship (±95% CI; p = 0.006).

Focal fish performed at least one HUD after aggression from the breeder male in 401 out of 611 instances (65.6%). The latency to the next aggression from the breeder male was greater when the receiving fish performed a HUD than when they did not ($F_{1,18.71} = 5.38$, p = 0.032; Fig. 2).

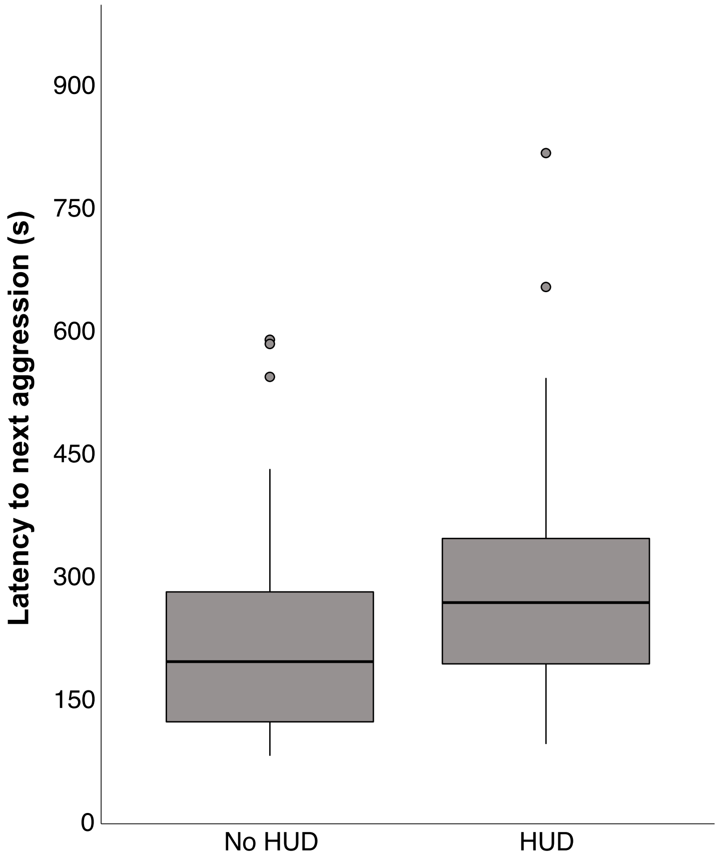

Figure 2. The median latency in seconds for the breeder male to next show aggression to the focal fish following aggression that elicited a head up display compared to aggression that did not. The time to the next aggression was greater when a head up display was produced (p = 0.032).

4. Discussion

Using detailed observations of replicate laboratory housed social groups of daffodil cichlids, we found that the head up display (HUD) is given in response to the majority of aggression performed by the most dominant group member and is seldom produced in the absence of aggression. We confirmed that the HUD serves as a signal of submission in this species, as has long been assumed (e.g., (Bergmüller & Taborsky, 2005; Grantner & Taborsky, 1998; Reddon et al., 2019; M. Taborsky, 1984)). Specifically, we found that when receiving aggression from the dominant breeding male, the time until the next instance of aggression depends on whether or not the receiving fish produces a HUD in response. When the receiver of aggression responds with a HUD, there is a longer average latency to the next instance of aggression from that dominant individual. The HUD may therefore avoid conflict, possibly by communicating a lack of motivation in the signaller to perpetuate or escalate an aggressive interaction. This submissive communication may be beneficial for both the sender and receiver as aggression is costly to all parties in terms of time, energy, and divided attention (Copeland, Levay, Sivaraman, Beebe-Fugloni, & Earley, 2011; Maan, Groothuis, & Wittenberg, 2001; Neat, Taylor, & Huntingford, 1998).

Occasionally, the focal fish in our study appeared to produce HUDs towards the dominant male without an obvious inciting aggressive act. It is possible that the apparently spontaneous HUDs we observed were in fact in response to subtle or obscured aggression from the breeder male (e.g., from behind a shelter out of view of the video recording). Perhaps HUDs are also occasionally shown after a longer delay following aggression, making them appear to be part of a distinct social interaction, or are given pre-emptively in an attempt to avoid future aggression (Bergmüller & Taborsky, 2005).

In some instances, fish do not show HUDs in response to dominant aggression, despite the apparent benefits of doing so. Little is yet known about the context specificity of submissive signal use in this species. Although HUDs appear to be beneficial, submissive behaviour does carry an energetic cost in this species (Grantner & Taborsky, 1998; M. Taborsky & Grantner, 1998), and in some scenarios it may be advantageous to avoid aggression, rather than showing submissive behaviour (Balshine et al., 2017).

There is also some variation in the expression of the HUD itself: for instance, the degree to which the head is raised in the water column varies from a subtle pivot upwards to the fish assuming a nearly perpendicular position. Other behaviours, such as tail or body quivering, may also accompany the HUD (Reddon et al., 2015), and the degree of lateral movement varies from being absent, through a gentle quivering of the tail, to a full body shake. This appears to correlate with the angle of the tilt in the water (AR pers. obs.), suggesting these elements could combine to indicate signal amplitude. In our current study, we did not measure variation in expression of HUDs including the presence or absence of tail quivering, and future work examining the meaning of variation in HUDs and the role of tail quivering during the HUD would be worthwhile. If HUDs do differ in their strength, it would be interesting to investigate under what conditions this variation is expressed. For example, it would be worth examining whether the receiver phenotype or the escalation level of the aggression received influence the expression of HUDs, or if the social context, such as the presence of potential eavesdroppers affects the expression of HUDs. The HUDs may be perceived by other group members, and in this context, it would be interesting to understand whether this behaviour can affect the aggression directed towards the signaller by non-target receivers. Alternatively, the expression of the HUD may depend on the signalling environment as more conspicuous or vigorous HUDs may increase signal transmission efficiency in a noisier or more complex signalling situation (e.g., (Bruintjes & Radford, 2013; Eaton & Sloman, 2011). These questions will need to be addressed in future studies in order to fully understand the complexity of agonistic communication in this highly social vertebrate.

In conclusion, our current findings demonstrate that the head up display in the daffodil cichlid acts as a submission signal and reduces the frequency of aggression from the receiver. This behaviour has long been assumed to have this function, but to our knowledge, this is the first demonstration that the HUD has this effect on the receiver. It is essential to understand communication within groups in order to understand the behaviour of social species (Frommen, 2020). Our results help to elucidate the nuances of agonistic signalling in this emerging model for the study of sociality and suggest future avenues for work on the communication system of this species.

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Data availability: The dataset required to produce the presented analyses and figures will be available on Mendeley Data.

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Fig 1

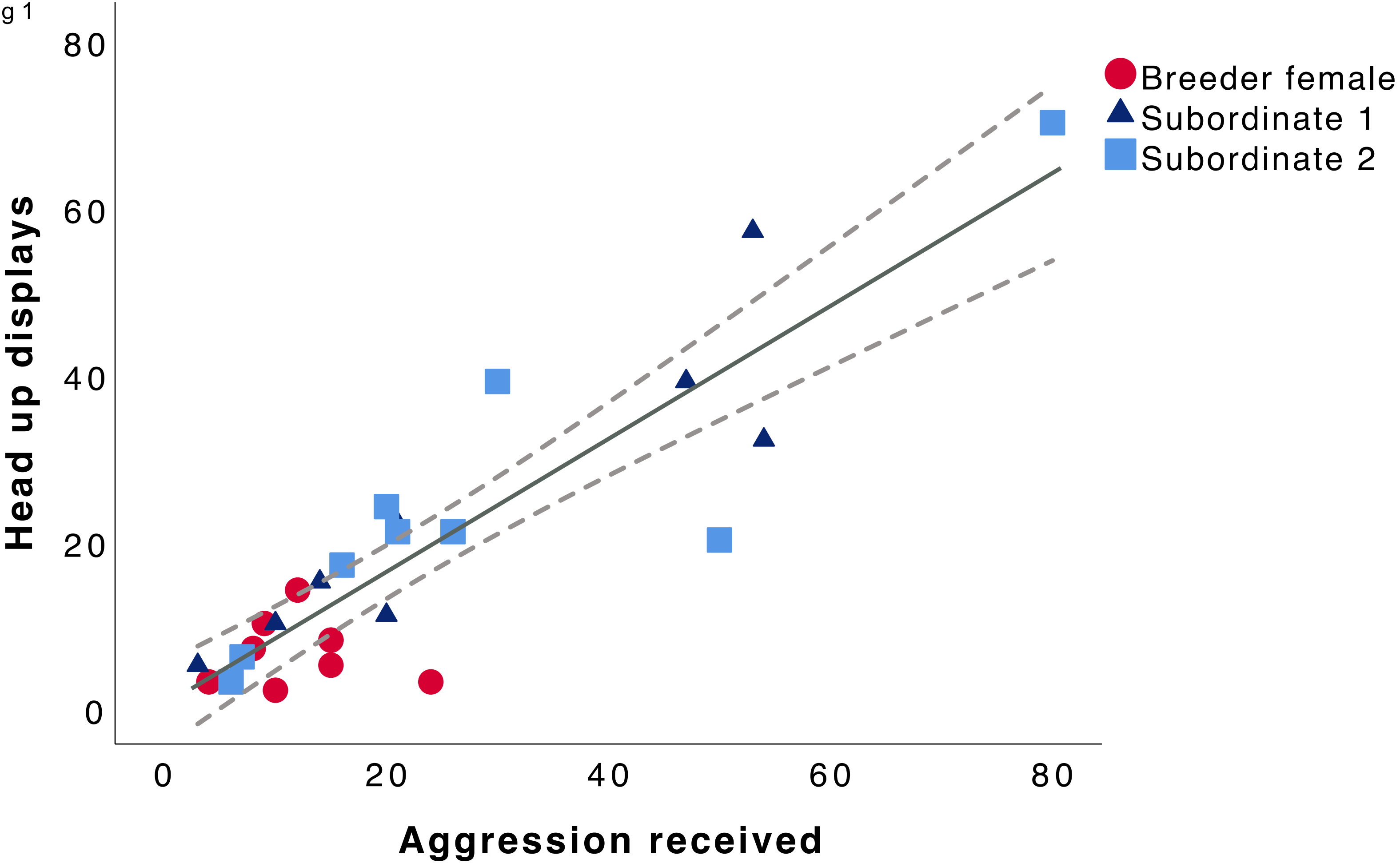
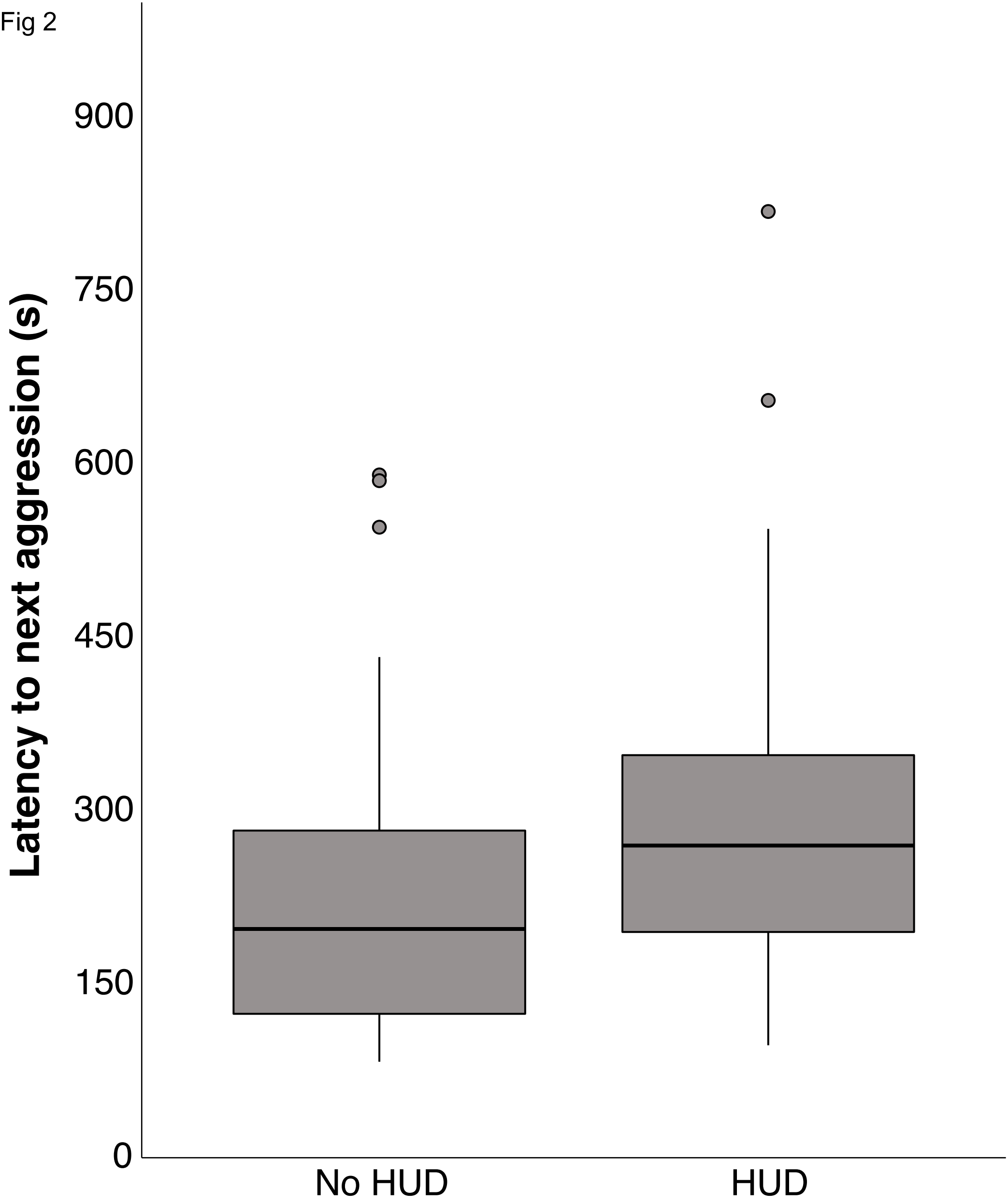

Head up displays
0
20
40
60
80
Aggression received
0
20
40
60
80
● Breeder female
▲ Subordinate 1
■ Subordinate 2

Fig 2


Latency to next aggression (s)
900
750
600
450
300
150
0
No HUD
HUD