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Shelter access is associated with subordinate submissiveness towards dominant males in a cooperatively breeding fish

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Abstract

Subordinate individuals within social groups vary in the degree to which they are tolerated by the dominant group members. Greater acceptance within the group can lead to improved access to crucial resources such as food or refuges from predation. Subordinate individuals may attempt to avoid conflict with dominant group members by showing submissive behaviours that signal deference and deescalate agonistic interactions. The role of submissive behaviour in increasing tolerance of dominants is often assumed but has rarely been explicitly examined. In the cooperatively breeding cichlid fish *Neolamprologus pulcher*, shelter access is vital for survival given the intense predation pressure experienced in Lake Tanganyika. We conducted behavioural observations on 23 laboratory-housed *N. pulcher* social groups and investigated whether there is a relationship between submissiveness of subordinates and shelter access within their group territory. We found that subordinates displayed more submission per aggression received in interactions with dominant males compared to dominant females, and those that submitted more to the dominant male were permitted to spend more time within the shelters at the core of the territory. No association was found between submission shown to female dominants and shelter access. These findings highlight sex-specific differences in how dominants mediate territory access and suggest dominant males may play a greater role in enforcing the social hierarchy in *N. pulcher* groups.

Keywords

aggression, daffodil cichlid, *Neolamprologus pulcher*, social tolerance, submission, subordination.

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1. Introduction

Group living can result in conflict between group members, especially under conditions of resource scarcity or reproductive skew (Rubenstein & Shen, 2009; Cant, 2012). Frequent conflict can be costly to the group, requiring energy, risking injury, decreasing productivity and cohesion (Aureli et al., 2002; Copeland et al., 2011; Goncalves & Radford, 2022a). To limit the costs of conflict, social groups are often organised into social hierarchies which set the priority of resource access including reproductive rights within the group (Drew, 1993; Haley et al., 1994; Beekman et al., 2003; Tibbetts et al., 2022; but see Packer et al., 2001). To avoid conflict with dominant group members, subordinate individuals may show submission signals which convey deference and deescalate agonistic interactions (Lewis, 2019). While submissive behaviour is often assumed to increase dominant tolerance of subordinate individuals, this function has seldom been directly examined (Reddon et al., 2022).

The Tanganyikan cichlid fish, *Neolamprologus pulcher* (commonly known as the daffodil cichlid, the fairy cichlid, or the princess cichlid), form complex social groups typically consisting of 3–15 adult and subadult individuals (Balshine et al., 2001; Heg et al., 2005). These groups exhibit cooperative breeding and are organised into linear dominance hierarchies based on body size (Balshine et al., 2001; Dey et al., 2013). Subordinate individuals help to care for the offspring of the larger, behaviourally dominant breeding pair by aiding in territory maintenance and participating in the defence of the territory against predators and competitors (Brouwer et al., 2005). Large social groups are beneficial to dominants as they increase territory quality and reduce dominant workload, thus improving dominants' reproductive success and reducing the chances of group extinction (Balshine et al., 2001; Brouwer et al., 2005; Wong & Balshine, 2011; Jungwirth & Taborsky, 2015). However, subordinates can also be costly to the dominants, as shown by a reduction in growth of dominant females in the presence of subordinates (Heg & Hamilton, 2008) and the occurrence of subordinate paternity (Hellmann et al., 2015, 2016). The degree to which dominants tolerate subordinates within the territory has significant implications for subordinate fitness prospects, as territories provide vital refuge from predators (Groenewoud et al., 2016; Freudiger et al., 2021), and subordinates that inherit breeding positions in their natal territories have higher lifetime fitness than those which disperse (Jungwirth et al., 2023).

Subordinate *N. pulcher* produce submission signals in response to aggression from those above them in the dominance hierarchy (Reddon et al., 2019) and these behaviours reduce dominant aggression (Ruberto et al., 2020). Bergmüller & Taborsky (2005) found that subordinates may pre-empt punishment from dominants using submissive behaviours, while Hidaka et al. (2024) showed that in the closely related *Neolamprologus savoryi*, the submissiveness of subordinates increases with dominant aggression levels, suggesting these behaviours are a response to within-group conflict. Taborsky et al. (2012) found that *N. pulcher* that were raised with older family members tended to show higher levels of submission and spent a larger proportion of time near the core of territory compared to individuals raised without older kin, suggesting that submissive behaviours may play a role in territory tolerance by dominants. La Loggia & Taborsky (2024) found that accepted subordinates tended to be more submissive than evicted subordinates, although the direct relationship between submission and dominant tolerance requires further examination. Submissive behaviours may act as a form of social currency (Reddon et al., 2022) exchanged for dominant tolerance and access to the vital shelters at the territory core (Ruberto et al., 2024), but this hypothesis requires testing.

The aim of the current study was to explore the relationship between subordinate submissiveness and tolerance by the breeding pair within the breeding territory in *N. pulcher* groups. Specifically, how the level of submission shown by subordinates relates to the time spent within the potential breeding shelters at the core of the territory. We predicted that subordinates which exhibit higher levels of submission per aggression received from the dominant pair would be more tolerated in the shelters at the core of the territory.

2. Methods

2.1. Group establishment and housing

Twenty-three *N. pulcher* social groups were housed at Liverpool John Moores University, each comprised of 4 to 8 individuals assembled from fish of unknown relatedness out of large stock holding aquaria. Each group consisted of a dominant breeding pair (sexed by examination of their external genitalia) and between 2 and 6 subordinates of unknown sex (many of these fish were too small to confidently sex by external morphology). Social groups were housed in 90 l aquaria (53 × 43 × 38 cm) as described in Reddon et al. (2024) for at least 4 weeks prior to video recording. No group had eggs or newly hatched fry at the time of data collection. Each aquarium was furnished with four terracotta caves (shelters) situated at the centre of the floor of the aquarium, a foam filter, a heater, thermometer, and 1–2 cm of fine coral sand. Water temperature was maintained at 27 ± 1°C and fish were fed five days a week with Tropical Tanganyika prepared fish flakes. The fish were maintained on a 12:12 h light cycle. The standard length (SL in mm) of each fish was measured using dial callipers following video recording.

2.1.1. Observations

Each group was video recorded for 2 h in total, spread across four 30-min recordings taken on four separate days over a 2-week span using a Sony AX700 video camera recording at 4 k/60 fps. Video recordings were taken between 10:00–15:00, at least 2 h after the lights came on and 5 h before lights out. Thirty minutes prior to recording, the filter, heater, and thermometer were removed to improve the observability of the fish on the videos. These items were immediately returned to the aquaria following recording.

For each video, 30-min focal animal continuous observations were carried out on the largest subordinate in each group, chosen for consistency with previous research (Ruberto et al., 2020, 2024; Manara et al., 2023; Hirons-Major et al., 2024; Reddon et al., 2024), ease of identification, and because dominance interactions occur more frequently at the top of the hierarchy (Dey et al., 2013). Fish were discriminated on video based on body size with the aid of a ruler included in the video recording. As a measure of dominant tolerance, the total time in seconds that the largest subordinate spent with at least half of its body within any of the four terracotta caves was recorded. All occurrences of submissive behaviours (head up postures and tail quiver displays) shown by the largest subordinate towards the breeding pair, and aggressive behaviours (chases, opercular flares, and bites) received by the largest subordinate from the breeding pair were recorded following the ethogram of agonistic behaviours found in Manara et al. (2023).

2.1.2. Statistical analyses

For each observed subordinate, we analysed the number of submissions per aggression received from the dominants, and the time that subordinates spent in shelters across the four observation periods (seconds in the shelters per hour of observation). To control for potential effects of body size on aggression and submission, we included SL of each subordinate and dominant fish in our analyses. Outliers were detected by calculating Z-scores at a threshold of |2.5|. One group was identified as an outlier (Z = 3.53) and excluded from further analysis reducing the number of groups examined to 22. All data were analysed using R v.4.5.0 (R Core Team, 2025) and RStudio v.2025.05.1 (Posit tTeam, 2025), and all data and code for the analysis can be found in the Supplementary material.

The number of submissions per received aggression was analysed with a linear mixed model using the ‘lme4’ R package (Bates et al., 2015), with fixed factors for dominant sex (male/female), dominant SL, subordinate SL, and with a random factor for social group. Fixed effects of the model were evaluated using likelihood ratio tests. Multiple regression was used to analyse subordinates’ access to shelters, with two separate models to test how this was affected by submission to the dominant males, and to the dominant females respectively. Subordinates’ time in shelters was the response variable in both models, and factors were the submissions per aggression received (for either the dominant male or the dominant female), dominant SL (for either the dominant male or the dominant female), and subordinate SL. The fit and assumptions of all models were confirmed by visual inspection of plots for linearity, homogeneity of variance, presence of outliers, collinearity and normality of residuals, using the ‘performance’ R package (Lüdecke et al., 2021).

3. Results

There was a significant effect of dominant sex on the number of submissions performed by subordinates in response to each aggression received ($\chi^2 = 8.612$, $p = 0.003$), as subordinates performed more submission to dominant males than to dominant females (Figure 1). The number of submissions was not significantly affected by either dominant SL ($\chi^2 = 0.173$, $p = 0.677$), or by subordinate SL ($\chi^2 = 0.034$, $p = 0.854$).

There was a significant overall relationship in the regression model analysing subordinate access to shelters and submission to dominant males ($F_{3,18} = 7.021$, $p = 0.003$, adjusted $R^2 = 0.462$). Subordinates’ time in shelters was positively predicted by their submission per aggression received from dominant males ($\beta = 163.3$, $t = 2.800$, $p = 0.012$; Figure 2A). Time in shelters was also negatively predicted by dominant male SL ($\beta = -11.5$, $t = -3.261$, $p = 0.004$), but not by subordinate SL ($\beta = -4.2$, $t = -1.163$,

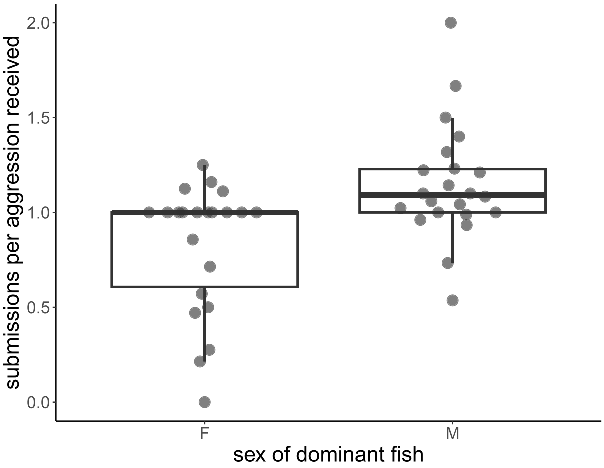

Figure 1. Boxplots with overlaid raw data showing the number of submissions performed by each observed subordinate in response to each aggression received from dominant female and dominant male *N. pulcher*. Subordinates showed more submission per aggression received to the dominant male compared to the dominant female ($p = 0.003$).

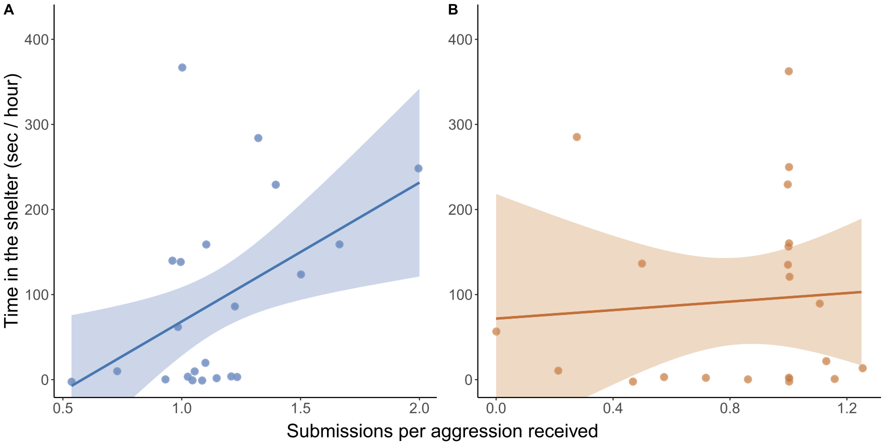

Figure 2. Scatterplots showing raw data for each observed subordinate of mean time in shelters against submissions per aggression received. The lines indicate the model-derived effects of the number of submissions per aggression received on subordinates' time in the shelters. Shaded areas represent 95% confidence intervals. Subordinates' time in shelters was significantly predicted by their levels of submission in response to aggression from (A) dominant males ($p = 0.01$; blue symbols), but not by (B) levels of submission to dominant females ($p = 0.76$; orange symbols).

$p = 0.120$). There was not a significant overall relationship in the model of subordinate access to shelters and submission to dominant females ($F_{3,18} = 0.499$, $p = 0.688$, adjusted $R^2 = -0.077$; Figure 2B), and there were no significant predictive effects on time in shelters of either submission per aggression received from dominant females ($\beta = 25.0$, $t = 0.317$, $p = 0.755$; Fig. 2B), dominant female SL ($\beta = -7.7$, $t = -1.027$, $p = 0.318$), or subordinate SL ($\beta = -1.3$, $t = -0.345$, $p = 0.734$).

4. Discussion

This study investigated whether there is a relationship between submission shown by *Neolamprologus pulcher* subordinates to the breeding pair and time spent by the focal subordinate within the potential breeding shelters at the core of the territory. We predicted that subordinates that displayed higher levels of submission to the breeding pair would be permitted to spend more time within the shelters. Fitting with this prediction, there was a significant positive correlation between submission shown to dominant males and shelter access suggesting that submission may increase tolerance from dominant males. Contrary to our predictions, there was no relationship between submission to dominant females and time spent in the shelters. These differences suggest that dominant males play an important role in regulating subordinate behaviour while dominant females may be less active in this regard.

Subordinates exhibited higher submission per aggression when interacting with dominant males compared to females and larger dominant males were associated with reduced shelter access. This may indicate that there is a greater perceived threat from the larger dominant males. These findings contrast with those of Hamilton et al. (2005) who found that subordinates were more submissive to relatively smaller dominant males and that dominant male size did not influence subordinate shelter entries. These differences may have been due to methodological variations. For example, we observed the largest helpers in the group only, while Hamilton et al. observed both large and small helpers from the same group. Additionally, unlike in our setup, the tank layout in Hamilton et al. allowed different groups to see one another, which may have influenced subordinate behaviour by increasing perceived social competition at the intergroup level (Radford, 2010; Goncalves & Radford, 2022b). In our study, dominant female body size did not significantly predict subordinate shelter access, further suggesting a more limited role in social enforcement for dominant females compared to dominant males. Hamilton et al. (2005) also did not find any significant effect of size disparity on subordinate interactions with the dominant female.

Gübel et al. (2021) found that, in the cooperatively breeding *Neolamprologus multifasciatus*, aggression by dominant females is influenced by spatial position within the territory, whereas dominant males show consistent aggression throughout the territory. If this sex difference in aggression was observed in *N. pulcher* as well, this may help explain the sex specific effects we observed as subordinates may perceive male aggression as more unpredictable or persistent, which may heighten the need for subordinates to signal submission to avoid conflict. In contrast, context-dependent aggression from females may result in subordinates exhibiting fewer submissive responses, especially if aggression occurs further away from the core of the territory. Subordinate *N. pulcher* alter their submissive behaviour depending on the spatial position within the territory (Reddon et al., 2024) and the number of shelters in the territory (Reddon et al., 2019; Ruberto et al., 2024). Dominant male *N. pulcher* are more aggressive than females (Ruberto et al., 2025), for example, Taborsky & Grantner (1998) showed that dominant males primarily spend time and energy on aggressive behaviours, whereas females are more engaged with territory maintenance and brood care.

It is puzzling that some subordinates show relatively low levels of submission despite the fact that submissive behaviour directed towards the dominant male correlates positively with access to the valuable shelters at the core of the territory. One potential explanation might lie in phenotypic variation along a helpful-submissive axis. Helping behaviour (e.g., excavating sand from the territory, aiding in defence against predators or competitors, and/or participating directly in brood care) may represent and alternative mechanism for appeasing the dominant breeders and increasing the degree to which a subordinate is tolerated (Bergmüller & Taborsky, 2005). Subordinates that are more submissive tend to invest less in helping behaviour and are also less likely to disperse away from their natal territory (Fischer et al., 2017; Antunes & Taborsky, 2020). Future studies should integrate measures of helping behaviour alongside submission to investigate the potential for a trade-off between helpfulness and submissiveness, and to further examine the possibility that some individuals ensure tolerance through help rather than submission.

The observed groups were maintained under controlled laboratory conditions. This is beneficial for standardising group composition and controlling for environmental variation. However, laboratory housed groups cannot fully capture natural social dynamics, due to the absence of ecological pressures such as intergroup competition and predation risk (Radford, 2010; Groenewoud et al., 2016). These factors have been shown to influence social cohesion and may promote greater tolerance of subordinates within breeding territories (Heg & Taborsky, 2010; Hellmann & Hamilton, 2018). Furthermore, our results are drawn from observations of unmanipulated social groups and therefore are correlational. Future studies should endeavour to apply an experimental approach, potentially by altering the social (e.g., Goncalves & Radford, 2022b) or physical environment (e.g., Ruberto et al., 2024) to further elucidate the relationship between submission and tolerance. Another approach might be to directly influence the production of submissive displays through pharmacological manipulations (e.g., Reddon et al., 2012) and measure the resulting effect on shelter access. These experimental results would help to further illuminate the role of submission signalling the maintenance of *N. pulcher* societies.

In cooperatively breeding species, group cohesion is critical for survival, reproduction, and predator defence, therefore it is essential to understand the factors that influence acceptance within social groups. This study demonstrates that subordinate submissiveness plays a context-dependent role in shaping dominant tolerance, influenced by the sex of the dominant individual. Specifically, submissive behaviours directed at dominant males were associated with increased access to shelters, suggesting that males may actively regulate subordinate shelter access, and therefore have an important influence over group composition and dynamics.

Supplementary materials

Data is available on https://doi.org/10.1163/1568539X-bja10341 under Supplementary Materials.

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