



Territorial behaviour and conflict management in a semi-social cichlid fish, *Neolamprologus caudopunctatus*

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Received 24 August 2021; initial decision 8 October 2021; revised 28 December 2021; accepted 13 January 2022; published online 8 February 2022

Abstract

Conflict solving strategies can prevent fights from escalating and reduce the costs of aggressive encounters. Having the capacity to efficiently assess an opponent's fighting abilities before fully committing to a fight is a useful social skill. Here, we conducted two experiments to investigate how a colony living, cichlid species, *Neolamprologus caudopunctatus*, changes its aggressive behaviour when faced with familiar vs unfamiliar opponents. First, we staged size matched, same-sex, dyadic resource contests and found that fights were always of low-intensity with neither familiarity nor sex influencing how quickly the conflict ended. Second, we explored the dual defence of mated territorial pairs together defending their territory boundaries against other pairs, either familiar or unfamiliar ones, and discovered that fights between two pairs were more vigorous, and that unfamiliar neighbouring pairs were attacked significantly more often than familiar pairs. We also observed that dark bars sometimes appeared on the sides of contestant's bodies, and that these bars were far more common in winners than in losers, suggesting that these might be visual signals of dominance. However, conflicts where contestants displayed bars were of longer duration than those without. Taken together, our results further advance our understanding of territoriality and conflict resolution strategies and set the stage for future studies focusing on how animals manage to co-exist in closely aggregated breeding territories and to form colonies.

Keywords

territoriality, Cichlidae, familiarity, resource contest, sociality, aggregate breeding, Lake Tanganyika, colony formation.

1. Introduction

Competition for resources (food, shelters, mates, territories, among others) can give rise to escalated aggressive encounters that can inflict tremendous costs (Preuschoft & van Schaik, 2000). How such conflicts are resolved will depend on the behaviour of both parties. While fighting can secure vital resources, it is costly in terms of energy, time, predation risk, and may lead to injury and even death (Smith & Price, 1973). To prevent these costs from escalating during a contest, animals can use different conflict resolution strategies. For example, being able to accurately and rapidly assess an opponent's strength or resource holding potential (RHP) enables a more precise estimation of the fight's potential outcome. Consequently, animals often have only a short physical interaction phase during a contest, or even prevent physical agonistic interaction altogether via displays that promote assessment (Hurd, 2006).

The regular interactions that occur with a known individual, such as a mate, or a neighbour, often result in a more efficient and accurate assessment of this individual's capabilities and motivation, facilitating better prediction for the outcomes of future interactions (Preuschoft & van Schaik, 2000). By observing or engaging in interactions, individuals can gain prior knowledge of an opponent's behavioural tendencies or fighting abilities and motivation which can also prevent costly fights (Enquist & Leimar, 1983; Preuschoft & van Schaik, 2000). Therefore contests with familiar individuals are expected to be shorter and less intense than contests with unfamiliar individuals (Höjesjö et al., 1998; Gómez-Laplaza, 2005). In many territorial species, neighbours usually represent a known and a reduced threat compared to strangers or intruders, who may be searching for a territory to breed in or a mate to breed with (Preuschoft & van Schaik, 2000). As such, familiar neighbours (who already have a territory of their own) are commonly tolerated to a greater extent than unfamiliar individuals (Temeles, 1994). This reduced aggression towards known neighbours is known as 'the dear enemy effect' (Fisher, 1954), a phenomenon widely observed across many taxa (Birds: Falls et al., 1982; Temeles, 1990; Briefer et al., 2008; Reptiles: Qualls & Jaeger, 1991; Whiting, 1999; Fishes: Frostman & Sherman, 2004; reviewed in Temeles, 1994).

The ability of a territory owner to discriminate between a familiar neighbour and an unfamiliar individual and then react accordingly with reduced

aggression towards the familiar neighbour is one type or a form of social recognition (Ward & Hart, 2003; Ward et al., 2007; Griffiths & Ward, 2011). Such familiarity recognition is a conflict solving strategy, and requires that individuals remember their opponent's identity, his or her social status, size and/or fighting ability relative to their own (Arnott & Elwood, 2008, 2009). Dominant/subordinate status and or winner/loser relationships are typically established when a fight ends, often when each opponent signals its status. Dominants will usually signal their intentions or their rank with elaborate displays (Clutton-Brock & Albon, 1979; Dufty, 1986; de Waal & Waal, 2007), with vocalization (Luo et al., 2017; Casey et al., 2020) or with bright colours (Setchell & Dixson, 2001; Butler & Maruska, 2015; Wiedemann et al., 2015). In contrast, losers can communicate their inferior status either by fleeing (Preuschoft & van Schaik, 2000), changing the colour of their body parts (paling or darkening) (O'Connor et al., 1999; Ligon, 2014; Bachmann et al., 2016; Ligon & McGraw, 2016), or by assuming subordinate postures or performing submissive behaviours (Bergmüller & Taborsky, 2005; Kutsukake & Clutton-Brock, 2008; Reddon et al., 2019).

In species that perform complex social behaviours such as group defence, cooperative hunting or cooperative care, efficient conflict resolution and recognition of individual group members are even more important and indeed are essential for group stability and productivity (Griffiths & Ward, 2011; Warburton & Hughes, 2011). In the cooperatively breeding and group living cichlid, *Neolamprologus pulcher*, it was shown that individual recognition occurs quickly (approx. 1 s) and that individuals use facial features to discriminate others (Balshine-Earn & Lotem, 1998; Kohda et al., 2015; Bachmann et al., 2016). Also, *N. pulcher* adjusts its fighting tactics and strategy depending on the familiarity of its opponent, reducing aggression towards familiar conspecifics and increasing submissive displays towards known individuals (Hick et al., 2014; Bachmann et al., 2016; Balshine et al., 2017; Reddon et al., 2019). In contrast, the closely related cichlid, *Telmatochromis temporalis*, a more solitary species that never forms groups, attacked familiar opponents as vigorously as unfamiliar ones (Hick et al., 2014; Balshine et al., 2017). These two cichlids' species represent two extremes of the social spectrum in the Lamprologine tribe of Lake Tanganyika.

Another member of this Tanganyikan cichlid tribe is the more socially intermediate species, *Neolamprologus caudopunctatus*, which does not live in groups, does not possess a size-based hierarchy, shows no cooperative breeding, but forms breeding colonies or aggregations. Aggregations contain anywhere from 5 to 100 breeding pairs, clustered densely together with a median nearest-neighbour distance of 66 cm (Schaedelin et al., 2012). Each pair defends a shelter where they raise young and hide to avoid predators or aggressive conspecifics. Non-breeding individuals gather in large shoals with up to 200 fish, lingering nearby the breeding colony (van Dongen et al., 2014). All non-breeding conspecifics, both adults and juveniles, are cannibals of young (Cunha-Saraiva et al., 2018). In the wild, *N. caudopunctatus* breeding pairs spend 60% of their time defending against such conspecific intruders as potential cannibals of young (Ochi & Yanagisawa, 1999). Hence, the ability to differentiate and act appropriately only to the true threats posed by intruders (who are conspecific cannibals) but not towards a lesser threat, nearby known neighbouring pair with offspring, would be valuable cognitive ability for *N. caudopunctatus*. Differentiating individuals that represent a different level of threat would save a breeding pair considerable time and energy. Therefore, in this study we investigated the type and degree of conflict solving strategies used towards familiar vs unfamiliar opponents by *N. caudopunctatus*, a cichlid species that is intermediate on the social behaviour spectrum.

To address how a colonial but non-cooperative species respond to conflict, we tested *N. caudopunctatus*' reactions to conspecifics in two different conflict situations, (1) resource contests between two sex and size matched opponents and (2) defensive interactions by territorial mated pairs against other territorial mated pairs as well as against small cannibalistic intruders. In the two experiments conducted, the contestants were either familiar or unfamiliar with each other. We predicted that *N. caudopunctatus*, as a semi-social species, would distinguish and respond differently to known individuals; both as pairs and as individuals they would behave less aggressively towards familiar versus unfamiliar individuals. Furthermore, we predicted that whenever two breeding neighbouring pairs are confronted with a nest intruder (i.e., non-breeding juvenile), they would attack the intruder together each pair defending their own nest, but that the group defence would reduce the per individual defence rate required to drive off the intruder.

2. Material and methods

2.1. General methods and housing conditions

The two experiments were conducted at the Konrad Lorenz Institute of Ethology, University of Veterinary Medicine Vienna, Vienna, Austria using wild *Neolamprologus caudopunctatus* caught at the southern tip of Lake Tanganyika, Africa. Experiment 1 was conducted in May of 2016, and Experiment 2 took place between April and July 2017. The fish used in Experiment 1 were housed in single sex 160 litres (80 × 50 × 40 cm) stock tanks each containing groups of 10–16 individuals for at least 14 days before being used in the experiment. The fish used in Experiment 2 were kept in the same stock tanks used in Experiment 1, however before this second experiment, fish were held in mixed sex groups for at least 14 days. Each stock tank contained 4–6 terracotta flowerpot halves that were used as shelters, 3 cm coral sand as substrate, a heater and one large sponge filter. The water temperature was maintained at $26 \pm 1^\circ\text{C}$. The fish were fed ad libitum six times per week either with frozen food (red mosquito larvae and *Daphnia* sp.) or with flake food for tropical fish and were kept under a 12/12 h light/dark cycle.

2.2. Experiment 1. Contests between familiar vs unfamiliar fish

We used 90 sexually mature *N. caudopunctatus* (44 females and 46 males) that were measured, and fin clipped to enable individual recognition. We staged resource contests between these fish in 45 litre (50 × 30 × 30 cm) aquaria, following protocols outlined in Hick et al., 2014, for two closely related cichlids. Familiar contestants came from the same stock tank, whilst unfamiliar contestants came from different stock tanks. The contest tanks were subdivided into three equal compartments with removable opaque plastic partitions (see Figure 1a for a schematic description of the set-up) and contained 2 cm of sand, a heater, a sponge filter and three flowerpot halves as shelter, one in each of the three compartments. The back and sides of the contest tanks were covered with opaque green sheets to reduce reflection and disturbance, and to increase the contrast on the videos by ensuring that these light-coloured fish could be easily spotted against the background.

Four contests were staged each day in a randomized order: one familiar and one unfamiliar contest for females and one familiar and one unfamiliar contest for males. At the beginning of each contest, two contestants of similar size and same sex were selected from the stock tanks. Thereafter,

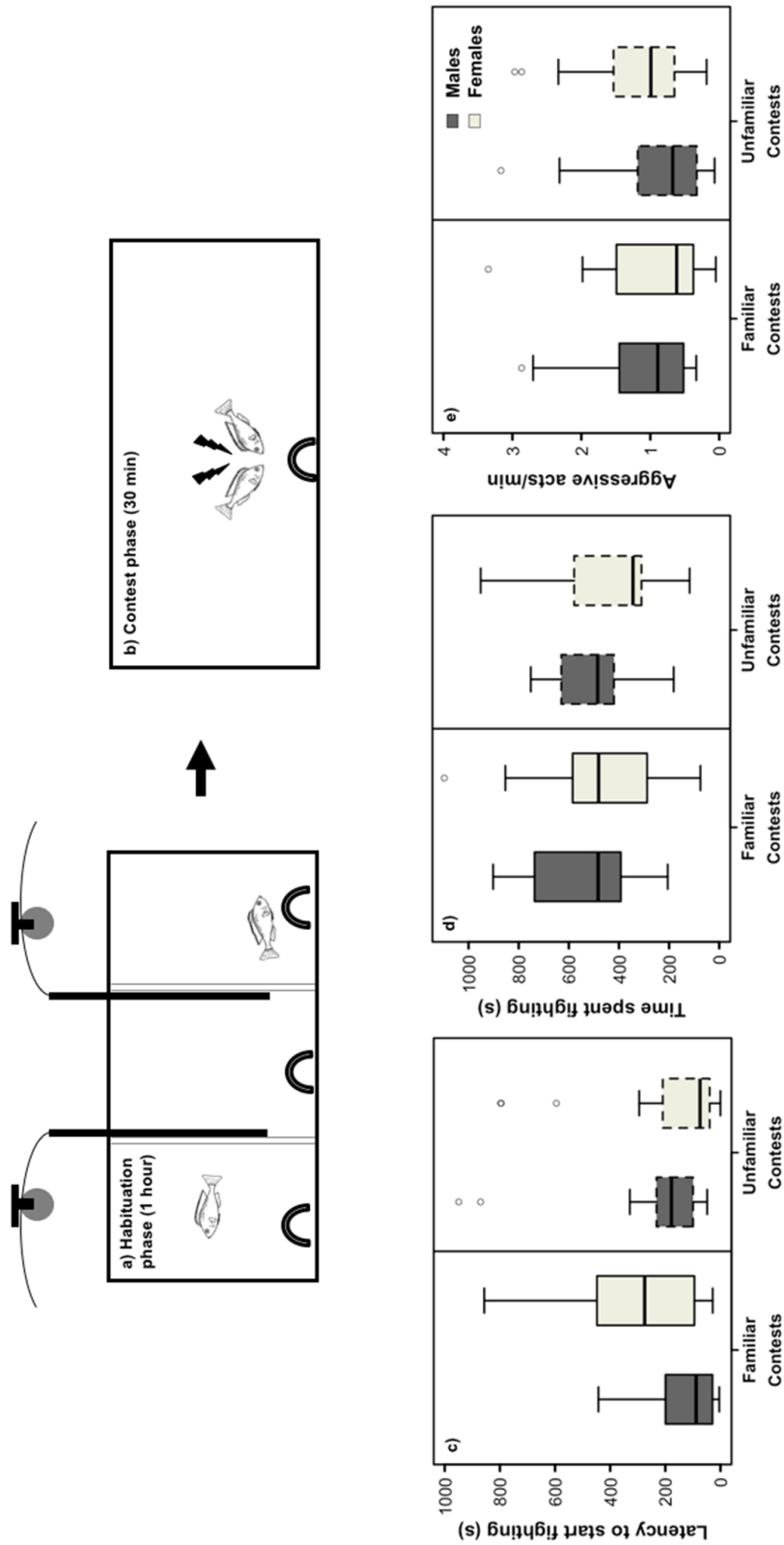


Figure 1. (Experiment 1) Schematic illustrations of the set-up for same-sex contests between familiar and unfamiliar fish. (a) The habituation phase: fish separated by an opaque partition (b) The observation or contest phase: the opaque partitions and the two end shelters are removed, and the fish can freely interact. Results showing (c) latency to begin fighting, (d) time spent fighting and (e) aggressive acts per minute for contests between familiar and unfamiliar contestants. Outliers are depicted as open circles. Males are in dark grey, and females are in light. * $p < 0.05$.

each contestant was placed individually in one of two outer compartments of a three-sectioned contest tank. Each fish had its own shelter, and neither fish could see the middle section or the other fish in the tank due to the two opaque partitions (see Figure 1a). While we made efforts to size match the contestants (Wagner, 2016), we were constrained by the sizes of fish available, on average contestants varied by 0.42 ± 0.33 g (range 0.005–1.1 g).

For each trial, the side containing the slightly larger individual was decided by coin toss. After a one-hour acclimatization period the two end shelters (flowerpots) were removed, and the two opaque partitions were lifted remotely via a pulley system allowing the contestant to see and interact with each other. Once the partitions were removed the fish could begin to fight with each other over the remaining central shelter (see Figure 1b). All trials were video recorded and had a 30-min duration; thereafter the fish were returned to a stock tank for used fish. Aggressive bouts were measured adopting the same procedure used by Hick et al. (2014) where an aggressive bout was considered to have started as soon a single aggressive act was initiated and a bout was considered to have ended when no additional aggressive behaviour occurred for at least 7 seconds. The total number of aggressive acts and aggressive bouts were tallied at the end of each trial.

All behaviour was scored from the video recorded trials by an observer who was blind to sex, identity and familiarity status of the fish in each contest. The behaviours recorded are described in detail in our species-specific ethogram (Table 1). For Experiment 1 we used Solomon Coder Version 16.06.26 to score behaviour and to analyse frequency, latency and duration of various behaviours. We compared the latency to start swimming after the removal of the opaque partitions, frequencies of aggression, submission, change in body coloration (depiction of bars) and the number of times each fish was 'in' the shelter, as well as duration of time each fish spent 'in' the shelter for both familiar vs unfamiliar contests. Total aggression, i.e., frequency of overall aggressive behaviours, was calculated by computing the sum of all performed aggressive displays and overt contact aggression performed throughout the trial. Due to the overall low intensity of aggressive acts observed (see below), to unambiguously assign a winner-loser status for each staged contest, we developed a set of rules. Winners were identified if they met two of the following three criteria: (1) displayed a higher frequency of overall aggression; (2) displayed a lower frequency of submissive acts;

Table 1.

The ethogram used to score the behaviours of *N. caudopunctatus* during the behavioural observation for both Experiment 1 and 2.

Type of behaviour	Description
Aggression (overt physical attacks)	
Ram	Focal fish touches another fish with its head or mouth region, jaws are closed.
Forced displacement	Focal fish approaches another fish, but opponent moves away.
Open mouth approach	Focal fish approaches another fish with an open mouth.
Mouth wrestle	Focal fish and its opponent lock jaws and push against one another in a reverse tug-of-war. Also known as mouth-fight.
Bite	Focal fish bites another fish
Bite/Avoid	Focal fish is about to bite another fish, but opponent is able to avoid.
Chase	Focal fish quickly darts towards another fish and follows this fish (swims after the other fish for several body lengths).
Aggression (displays)	
Fin spread	Focal fish spreads out all its fins including dorsal fins. Such fin spreads can occur while focal fish is next to (parallel) or while circling around its opponent, this display is also called lateral or parallel display.
Frontal display/Puffed throat	Focal fish spreads its opercula and lowers its jaw. Mostly occurs in combination with fin spread and/or an approach. Display is also known as opercula flare.
Approach	Focal fish approaches opponent with closed jaws, as if about to ram, but without any physical contact.
Head down	Focal fish lowers its head and raises its tail, sometimes in front or alongside of its opponent. This display is shown during courtship and territory defence.
Bars	Focal fish shows black stripes on its body and has black coloured eyes, mostly in combination with fin spread.
Head down and bars	Focal fish lowers its head and raises its tail with fin spread, black coloured eyes and black stripes on its body, sometimes in front or alongside of its opponent. Also shown during courtship and territorial patrol.
S-bend	Focal fish bends its body lateral in an S-curve towards another fish.
Pseudo-mouth wrestle	Both fish move back and forth while facing each other, as if about to mouth wrestle, but no physical contact is established.

Table 1.
(Continued.)

Type of behaviour	Description
Submission (flees)	
Flee	Focal fish quickly swims away for more than one body length.
Submission (display)	
Set back/Avoid	Focal fish retreats or displaces slowly from another fish.
Tilt	Focal fish tilts its body towards opponent, exposing the belly. Also known as 'head up display' (Ruberto et al. 2020)
Locomotion	
Sit	Fish touches the ground with its abdomen.
Swim	Slow locomotion using the pectoral fins.
In Shelter	Fish remains inside the shelter.
Freeze	Fish stays motionless on the ground or in a hiding; behaviour seen after releasing a fish in a new tank
Territory maintenance/breeding	
Brood chamber	Focal fish enters the shelter.
Sand transport	Focal fish takes a mouthful of sand and swims to either the breeding shelter or to an area right near the breeding shelter before spitting it out.

This ethogram is based on one described in Cunha-Saraiva et al. (2018) and was specifically designed for *Neolamprologus caudopunctatus*.

and (3) spent more time inside the shelter (measured as a duration in seconds). So, if both opponents spent an equal amount of time inside the shelter, then an individual was identified as the winner if it had a higher frequency of aggression and lower frequency of submission compared with its opponent. If the contest could not be called based on the rules described above, then the contest was classified as a tie, which occurred in 3 out of the 45 staged contests.

2.3. Experiment 2. Experimental housing

The effect of familiarity on territory defence was also tested by examining a more ecologically relevant context where a bonded pair of nest owners could defend their territories against either a familiar or unfamiliar neighbouring pair. This scenario is commonly observed in breeding territories in Lake Tanganyika (Ochi & Yanagisawa, 1999, FS, pers. obs.). We used four large experimental tanks (400 litres, 129 × 65 × 50 cm), which were divided

into four separate spatially distinct compartments by perforated, transparent partitions (Figure 2a). The perforated clear partitions allowed both visual and olfactory contact between individuals across the compartments. Each compartment had its own small filter and half flowerpot that could be used as both shelter and breeding substrate. Two pair-bonded pairs, that had naturally formed in the large mixed sex stock tanks (see above), were captured and placed in the two central compartments of the experimental tanks. Thus, each of the two central compartments housed one naturally formed pair-bonded pair each pair with its own shelter, while the two end compartments were left empty of fish. This arrangement served to provide a visual continuum of potential breeding territories and avoided the edge effects, of dampened aggression, observed in an earlier study (Schädelin et al., 2012) (see Figure 2a for a schematic description of the experimental set-up). We checked daily for the presence of eggs to ensure that defence motivation was not influenced by the presence of offspring. In total, we used 160 fish (80 male and female pairs) in this experiment (Experiment 2). Males in each pair were always slightly but recognizably larger than the female (average body length difference 6.9 ± 4.8 mm), enabling us to identify each fish during video coding. The sexual dimorphism in this experiment also mirrored the degree of sexual dimorphism observed in wild pairs (Schädelin et al., 2015). One of the two pairs that were placed in each experimental tank was randomly assigned to be the focal pair ($N = 40$) and the other pair was assigned to be the stimulus or neighbouring pair ($N = 40$). The behavioural observations of both pairs in each trial were video recorded. The behavioural data obtained from the focal pair-bonded pair was analysed as the dependent variable, and the behavioural data from the neighbouring stimulus pair was used as a covariate in the analysis. The observer was aware of the familiarity status while coding the behaviour but was not aware of whether the observed pair was a stimulus or a focal pair.

2.3.1. Experiment 2a. Defence towards intruders with and without neighbours

One week after the established pairs had been transferred into their respective compartment within the large four chamber experimental tanks, we video-recorded the pairs for 10 minutes and this was followed by a 2-min nest defence assay which was also video recorded. The nest defence assay was conducted by placing a transparent plastic tube holding three juvenile

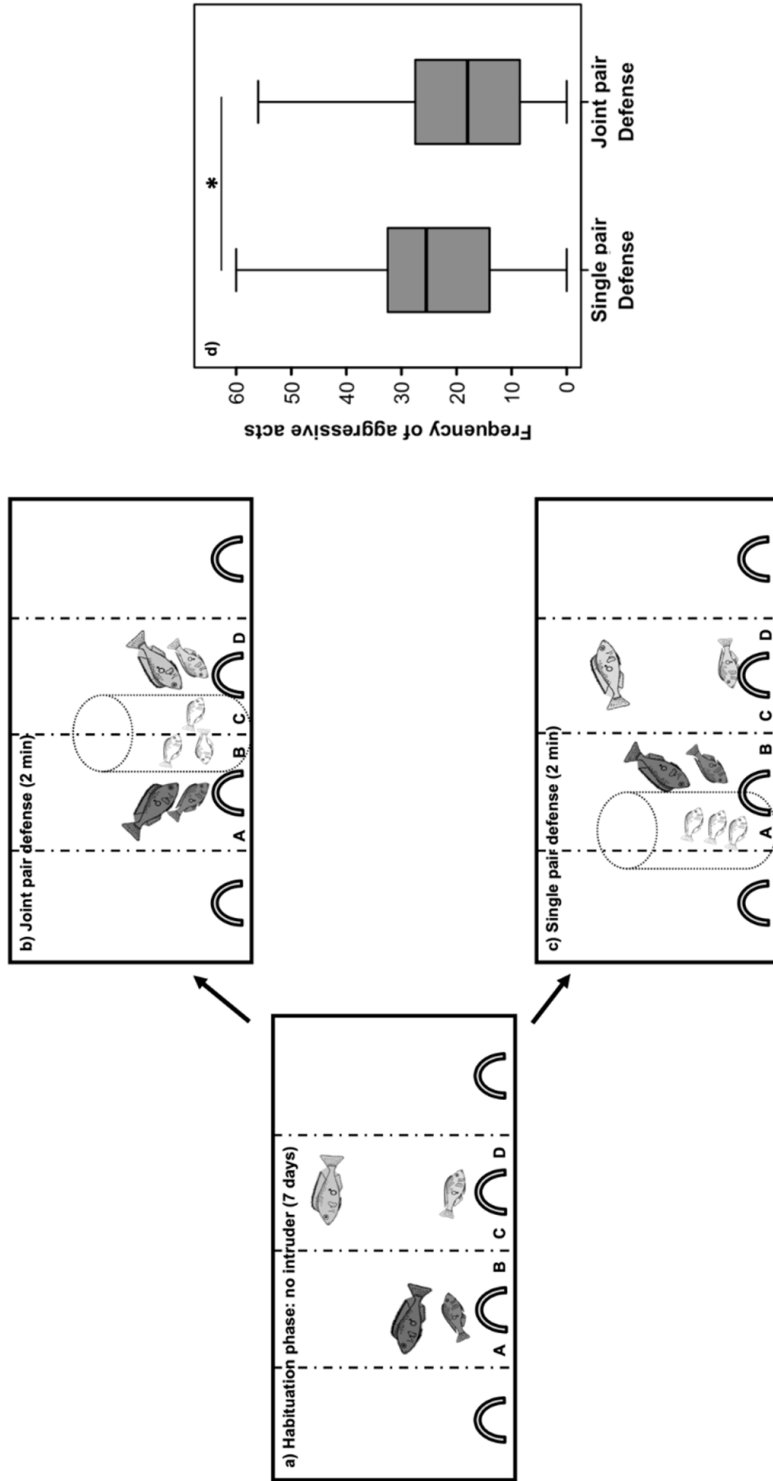


Figure 2. (Experiment 2a) (a) A schematic illustration of the experimental set-up. Vertical dashed lines represent the plexiglass partitions. Dark grey fish represent focal fish; light grey fish are the neighbours. (b) A schematic illustration of what the joint pair defence set-up looked like when the intruders were placed near the territory boundary between the two neighbouring pairs; (c) A schematic illustration of the single pair defence set-up when the intruders were placed far away from the neighbouring pair, and only the focal pair could defend; (d) Results: Aggressive acts performed by the focal pairs under single and joint pair defence scenarios. We tested 80 pairs (40 females and 40 males) in this experiment. Positions of the intruder test are depicted on the figure as A, B, C and D. Male and females combined is depicted on the figure. * $p < 0.05$.

conspecifics in one of four different possible tank locations (placed in positions A, B, C, or D, see Figure 2b, c). The intruder tube was perforated so that olfactory as well as visual cues of the three juvenile conspecifics could be easily transferred. Juvenile *N. caudopunctatus* eat young and are actively defended against by breeding pairs in both field and laboratory studies (Ochi & Yanagisawa, 1999; Schaedelin et al., 2012; Cunha-Saraiva et al., 2018). Hence with this intruder test we could experimentally elicit defence behaviour and standardize the degree of threat while observing and quantifying the focal pair's investment in defence. We also could compare what happens to defence activities when the intruder tube was placed next to only the focal breeding pair's territory (in position A or D, leading to only the focal pair being able to defend) versus when the intruder tube was placed between the territories of the two pairs, just next to the transparent partition between the two neighbouring pairs, leading to joint pair defence (in positions B and C, see Figure 2b, c). Trials always took place in the morning between 9 and 12 am to avoid any diurnal effects on behaviour (Desjardins et al., 2011).

2.3.2. Experiment 2b. The influence of a new neighbour on territorial defence

Seven days after the two neighbouring pairs had established side by side territories in a large experimental tank (Figure 3a), we video-recorded all behaviours for a 10-min period before starting the 2-min defence assays (Experiment 2a). Thereafter, we conducted the following test: in the evening, an opaque partition was placed between the two pair-bonded pairs; then the 7-day acclimatized neighbouring pair to the focal was captured using a hand net and replaced with an unfamiliar pair ($N = 40$) (Figure 3b). Thus, focal pairs were housed overnight with unfamiliar neighbours (new neighbours that remained behind opaque solid partitions). In the next morning, the opaque partitions were removed, and the neighbours were revealed. This overnight acclimatization period is sufficient for cichlid breeding/pair-bonded pairs to establish a territory (Balzarini et al., 2014). We video-recorded all behaviours performed for 10 min after the opaque partitions were removed and quantified the focal pair responses to the unfamiliar neighbouring breeding pair. Thereafter, we performed another defence assay using the same procedure as described above in Experiment 2a with three juvenile *N. caudopunctatus* as intruders. Focal pairs were observed and compared in terms of their responses to familiar neighbours on Day 7 and unfamiliar

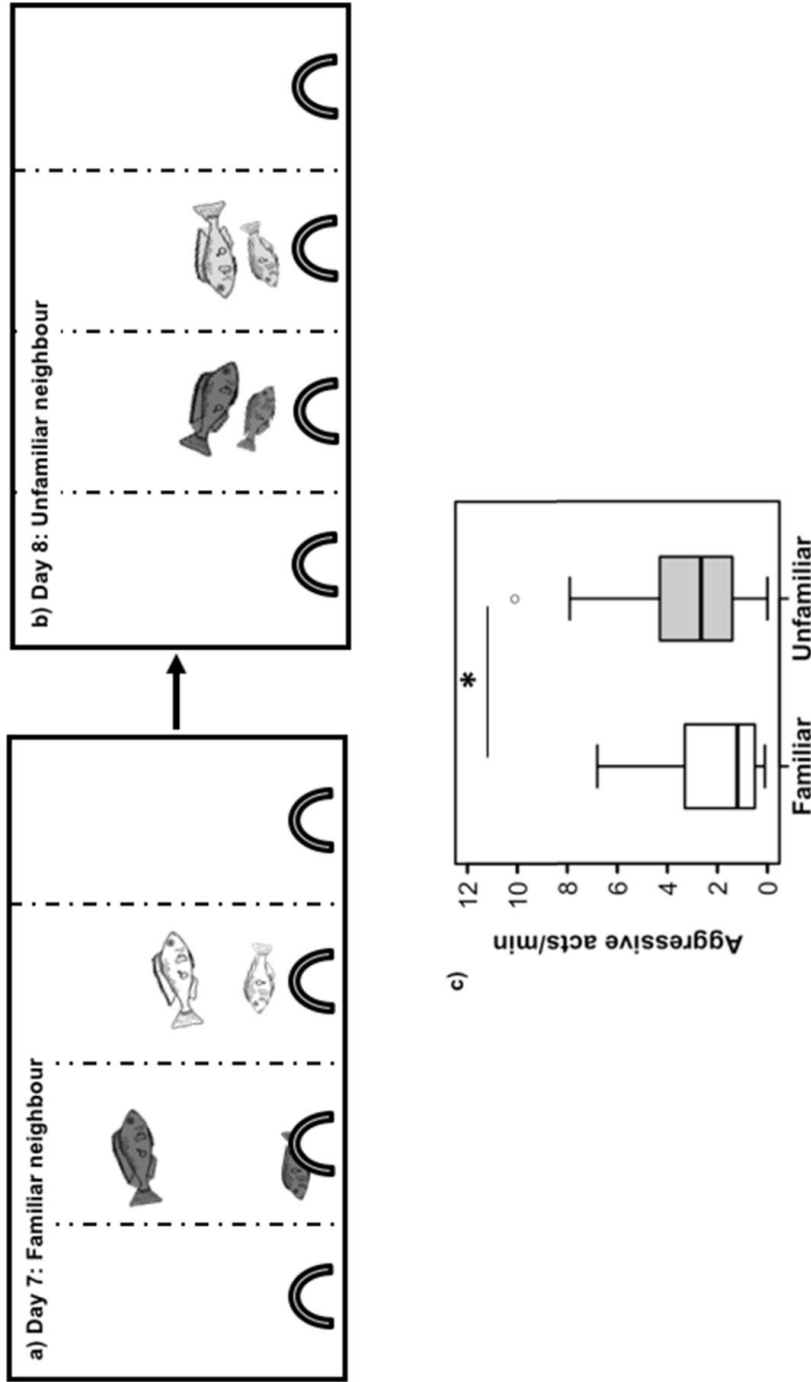


Figure 3. (Experiment 2b) Schematic illustrations of (a) the 7-day habituation phase; and (b) the new neighbour test phase on Day 8. In these two figures, different colours represent different breeding pairs with fish in dark grey representing the focal breeding pairs, fish in light grey representing a familiar neighbouring pair and white fish representing an unfamiliar neighbouring pair. (c) Aggressive acts performed before and after the manipulation in the new neighbour test phase. Light grey bars represent the before manipulation (familiar breeding pair) while white bars represent the after the manipulation (unfamiliar breeding pair). We tested 40 pairs (20 females and 20 males) in this experiment. Males and females have been combined. Outliers are depicted in the figure as open circles. * $p < 0.05$.

neighbours on Day 8 as well as how they responded towards the juvenile intruders before and after the manipulation.

All trials were videotaped and the behaviour of all four fish was scored by an observer who was blind to the familiarity status of the observed fish. For all parts of Experiment 2, a and b, the behaviour in the videos was coded using BORIS (Friard & Gamba, 2016) the behaviours scored are described in our species-specific ethogram (Table 1). All behaviours were treated as instantaneous events during video coding, except ‘freeze’ (where the fish sits on the ground), for which we measured the duration of the freezing act. For the analyses we summarized behavioural frequencies into the three main categories: aggression towards the: (1) territory intruders, (2) neighbouring breeding pairs and (3) breeding partner. We also calculated the latency to start attacking the intruders and to interact with the neighbouring breeding pair.

2.4. Statistical analysis

We used the statistical software R (Team, 2019 version 3.6.1) to perform the analyses. Prior to any statistical analysis, normality was determined by visual assessment of the data distribution through a histogram coupled with a Shapiro-Test to statistically confirm the visual interpretation while heterogeneity was determined by performing a Levene test for homogeneity of variances. Whenever necessary data was transformed.

2.4.1. Experiment 1

A total of 42 of the 45 contests resulted in a clear winner and loser. The remaining three trials were undecided and not included in the subsequent analyses. We also opted to remove one outlier from the data analysis concerning the latency to start fighting variable, following the result provided by the Grubbs test ($G = 5.28$, $U = 0.65$, $p < 0.001$, we were blind to the familiarity and sex of individuals while conducting this outlier test; outliers package 0.15). Prior to analysis, latency to start fighting, total aggression, and duration of the aggressive display phase were Box–Cox power transformed to meet normality and homoscedasticity requirements, whereas contest duration was normally distributed and thus not transformed. Using the MASS package 7.3-45 (Venables & Ripley, 2013), we plotted a range of potential power parameters against their log-likelihood and visually identified the maximal λ value (latency to start fighting, $\lambda = 0.26$; total aggression, $\lambda = 0.30$; duration of aggressive display phase, $\lambda = 0.34$); we used these

values when using the box-cox transformed model. To determine how familiarity (familiar vs unfamiliar) and sex (male vs female) and their interaction influenced the winner's latency to start fighting, overall contest duration and the duration of aggression, we used a factorial ANOVA (`aov` function from the `stats` package) and to control for the interdependency of the winner's and loser's behaviour we have included the loser's behaviour as a covariate. Model assumptions were verified using the diagnostic plots and by assessing the distribution of the residuals. We performed a linear regression analysis to infer which factors may influence the duration of aggressive bouts: the latency to start swimming after the opaque partition was removed, contest intensity (i.e., total aggression) and latency to start fighting. Finally, to investigate if changes in body coloration (depiction of bars) is used as a dominance signal, we characterize body darkening behaviour as present or absent. To investigate if the appearance of bars was specific to winners or losers, we performed a logistic regression using the `GLM` function from the `stats` package with a binomial distribution.

2.4.2. Experiment 2

In Experiment 2a, to test the effect of the neighbour's familiarity (familiar vs unfamiliar), sex (male vs female) and intruder position (single vs joint defence, Figure 2a) on territory defence, we performed linear mixed models (`lmer` function from the `nlme` package) with a gaussian distribution. Furthermore, to investigate the potential benefit of joint defence, we applied a non-parametric approach (Wilcoxon signed-ranks test) to compare the sum attacks of both focal and neighbouring territorial pairs together against solo pair defence. In Experiment 2b, we used linear mixed models (`lmer` function from the `nlme` package) with a gaussian distribution to test the effect of experimental phase (before vs after manipulation) and sex (male vs female) on aggression towards the neighbouring pair (behavioural data was transformed when necessary to reach normality), latency to approach the neighbouring pair and territory defence against intruders. We also included pair identity as random effect to control for individual variability. Each model was validated by assessing the distribution of the model's residuals and choosing the model with the lowest AIC score (Johnson & Omland, 2004).

2.5. Ethical note

The procedures in this study were discussed and approved by the University of Veterinary Medicine Vienna's institutional ethics and animal welfare

committee and are in accordance with Good Scientific Practice guidelines and national legislation of Austria (Experiment 1: ETK-02/01/2016, Experiment 2: ETK-15/03/2017).

3. Results

3.1. Experiment 1. Contest outcomes and dynamics

A similar number of contests fought by males and females in each familiarity context, familiar ($N = 21$) and unfamiliar ($N = 21$), resulted in a clear winner (Yates corrected chi-squared test: $\chi^2 = 1.52$, $p = 0.21$). Contests commonly began by both competitors freezing and the contestants would typically start to fight after an average of 204.9 s had elapsed (the range of latencies to the first aggressive display/attack was 0.20–949.4 s). There was no effect of familiarity, sex or the interaction between the two on the onset of fighting (Table 2, Figure 1c). Contest duration was similar for familiar and unfamiliar contests (Table 2, Figure 1d), and for male and female contests (Table 2, Figure 1d). Latency to start swimming again following the freezing response, did not predicted the overall duration of the aggressive bouts (LM: $r^2 = -0.03$, $F_{1,37} = 2.32$, $p = 0.13$) or the latency until first interaction between contestants (LM: $r^2 = -0.01$, $F_{1,37} = 0.61$, $p = 0.43$).

Following the initial brief freezing period described above, contests were composed of distinct bouts of aggression. On average, there were 26 distinct bouts per contest, each bout lasting on average for 24.6 s (range 5.9–107.4 s). The contest intensity (i.e., total aggression) was not influenced by familiarity (Table 2, Figure 1e), sex (Table 2, Figure 1e), nor was there a significant interaction between the two main factors (Table 2, Figure 1e).

Contests consisted of mostly non-contact aggressive displays (median = 0.82 display/min, range 0.05–3.3 acts/min) and very few overt contact aggressive acts (median = 0 acts/min, range 0–0.26 acts/min). Overall, contest intensity was low, with aggressive displays (raised fins and the head down posture) comprising 99% of the aggressive behaviour observed. Familiarity, sex and the interaction between familiarity and sex together did not influence the duration of the display phase (Table 2).

Furthermore, in 23 out of 84 observed fish (27.4%), dark bars appeared on the bodies of contestants during the trials. These bars might signal

Table 2.

Factorial ANOVA analysis (Experiment 1) of the potential effect of Familiarity (Familiar vs. Unfamiliar), sex (Male and Female), the interaction and the loser's behaviour on the winner's behavioural output during the contests: latency to start fighting, contest duration, contest intensity and display phase.

Source	df	<i>F</i>	<i>p</i>
Latency to start fighting			
Loser's behaviour	1	35.27	<0.001***
Familiarity	1	1.30	0.26
Sex	1	0.20	0.65
Interaction	1	0.93	0.33
Residuals	37		
Contest duration			
Loser's behaviour	1	19.20	<0.001***
Familiarity	1	1.83	0.18
Sex	1	0.19	0.66
Interaction	1	2.05	0.16
Residuals	37		
Contest intensity			
Loser's behaviour	1	11.13	0.001***
Familiarity	1	0.37	0.54
Sex	1	0.77	0.38
Interaction	1	0.0008	0.97
Residuals	37		
Display phase			
Loser's behaviour	1	27.98	<0.001***
Familiarity	1	0.80	0.37
Sex	1	1.08	0.30
Interaction	1	0.001	0.96
Residuals	37		

Significant *p* values are marked with asterisks.

dominance in *N. caudopunctatus*, as winners took on stripes more often than losers (GLM, Contest Outcome: estimate \pm error = 1.44 ± 0.61 , $Z = 2.36$, $p = 0.01$) independent of familiarity (estimate \pm error = 0.02 ± 0.57 , $Z = 0.03$, $p = 0.97$) and sex (estimate \pm error = -0.44 ± 0.58 , $Z = -0.76$, $p = 0.44$). However, bar presentation was also associated with longer contests (GLM, Contest duration: estimate \pm error = 0.003 ± 0.001 , $Z = 3.09$, $p = 0.001$). The average length of a contest when contestants had bars was 771 s, while contests without bars lasted on average only 469 s.

3.2. Experiment 2a. Defence towards intruders with and without neighbours

Focal pairs performed more aggressive acts against intruders when they had to defend as a single pair vs when two pairs acted together to fight against intruders (LMM: $\chi^2 = 5.96$, $p = 0.01$, Figure 2d), independent of the neighbouring pair's aggressive behaviour (LMM, $\chi^2 = 2.47$, $p = 0.11$). Although mated pairs always attacked the intruders more when defending alone, the sum attacks on intruders by two pairs of *N. caudopunctatus* was considerably greater than the attacks elicited by solo pairs (Wilcoxon signed-ranks test: $W = 2266$, $N = 80$, $p < 0.001$), suggesting a shared defence could be a benefit that selects for colony formation. In general, males defended more vigorously than females (LMM, $\chi^2 = 10.04$, $p = 0.001$).

3.3. Experiment 2b. How does having a new neighbour influence territorial defence?

Focal pairs reacted more quickly and more aggressively when interacting with an unfamiliar neighbouring pair (on Day 8) in comparison to their behaviour with a familiar pair (on Day 7) (Latency to approach neighbour: LMM, Familiar vs Unfamiliar, $\chi^2 = 65.8$, $p < 0.001$; Aggression towards neighbours: LMM, Familiar vs Unfamiliar, $\chi^2 = 4.83$, $p = 0.02$; Figure 3c). This was true for both males and females (Males vs Females, $\chi^2 = 0.71$, $p = 0.39$). The attack frequency towards intruders (the trio of conspecific juveniles) was not influenced by the 'new neighbour' familiarity manipulation (LMM, $\chi^2 = 1.50$, $p = 0.21$).

4. Discussion

In this study, we examined resource competition and resource defence in the semi-social, biparental cichlid *N. caudopunctatus*. Contests over shelter were substantially less intensive than the behaviour observed in other related cichlid species (e.g., *Neolamprologus pulcher* and *Telmatochromis temporalis*) and single fish were equally aggressive towards familiar and unfamiliar opponents. However, bonded pairs attacked unfamiliar neighbouring pairs more vigorously than familiar ones. Pairs also attacked intruders more intensely when they were defending on their own, compared to when attacking alongside a neighbouring pair, i.e., when the intruder was at a

shared territory boundary. At the shared territory boundaries, four fish working together had higher overall attack rates on intruders but the per fish attack rate was lower when four fish (two neighbouring pairs) attacked intruders together.

The contests between two single fish were not vigorous, and conflict resolution was much less obvious compared to identically staged contests with other related cichlids (Hick et al., 2014). The criteria used to assign a winner and a loser for each contest were more complex than what was necessary with *N. pulcher* and *T. temporalis*, where most of the contests ended unequivocally with a clear loser and winner (Hick et al., 2014). Furthermore, the degree of competitive behaviour performed by single fish was neither influenced by the degree of familiarity nor by the sex of the competing dyad. No sex difference in contest behaviour might be expected in this monomorphic and biparental species as both sexes require protective shelter. However, the lack of an impact of familiarity on these fights over a shelter was unexpected since *N. caudopunctatus* breeds in dense aggregations where modulating aggression according to the identity, capabilities and motivation of an opponent should result in considerable energy and risk reduction benefits.

In our first contest experiment, the fish were not paired and unpaired *N. caudopunctatus* typically live-in schools (van Dongen et al., 2014), are not territorial and do not defend shelters. Therefore, it is possible that the mere presence of a valued resource, a shelter, for 1 hour was insufficient motivation to engage in potentially costly conflict for *N. caudopunctatus*. In Lake Tanganyika, shelter is critical for *N. caudopunctatus* because these small fish have few means to defend themselves, and they live in areas of high predation pressure where competition for breeding shelters is high (Groenewoud et al., 2016). During our laboratory experiment, the motivation to invest in shelter acquisition and defence could have been dampened because predation was absent from our laboratory setting. Additionally, since we staged contests between same-sexed fish, and housed fish only with same sex conspecifics, the absence of a reproductive opportunity (i.e., a potential mate) in our experimental design may have also further dampened the motivation to fight for shelter which is used not only to hide from predators but also for breeding. Furthermore, the time to establish territoriality was rather short (1 h). However, such short testing time frames and the absence of a potential mate or predation risk did not hinder two other ecologically similar, sympatric cichlid species, *Neolamprologus pulcher* and *Telmatochromis temporalis*, from

establishing territorial behaviour and forcefully fighting one another for shelter possession (Hick et al., 2014). Nonetheless, future studies are now needed to assess the temporal dynamics of territoriality in *N. caudopunctatus* and should employ different residence durations. Only by understanding how territoriality is established can we begin to unravel how motivation plays a role in securing and maintaining these important resources.

In our second experiment we investigated aggressive behaviour of established pairs, the life stage when this species defends a breeding shelter and protects offspring. *N. caudopunctatus* pairs attacked intruders less when they were at a shared territorial border, compared to when the danger was at a border without neighbours. However, the joint defence by two pairs resulted in higher overall defence against intruders. Commensal defence behaviour is beneficial (Ochi & Yanagisawa, 1998) and may explain why animals such as *N. caudopunctatus* chose to live in dense breeding aggregations (Côté & Gross, 1993; Krause et al., 2002). Support for this idea comes from a previous study where in *N. caudopunctatus* pairs searching for a breeding territory preferred to settle close to an already established breeding pair rather than next to an empty territory (Schädelin et al., 2012).

In contrast to our first experiment with single fish where familiarity did not matter, in our second experiment with paired fish, we observed higher attacks rate towards unfamiliar neighbours. At the same time the attack rate towards small, conspecific intruders remained constant, which suggests that the difference in attack rate towards neighbours was indeed based on familiarity recognition. Such a reduction in aggression to familiar individuals is called ‘the dear enemy effect’ and would be expected when strangers pose a greater risk to territory owners than familiar neighbours who only trespassed accidentally on an established territory boarder (Temeles, 1994). The same dear enemy effect has been observed in many other animals, including *Juli-dochromis transcriptus* (Matsumoto et al., 2020) and *N. pulcher* (Sogawa et al., 2016; Sogawa & Kohda, 2018), two other sympatric cichlids from the same cichlid tribe.

N. caudopunctatus typically have a light beige/ grey body colour with a yellow or orange coloured dorsal fin and blue eyes. The forming of ‘bars’ or the darkening of eyes and body in *N. caudopunctatus*, is often observed in the wild when the fish patrol their territory or engage in agonistic interactions (i.e., mostly escalated ones) but also during natural and artificial stressful events (i.e., sickness, handling) (*personal observation FCS, FS, EW, CF*).

In Experiment 1 the probability of body darkening (e.g., the depiction of dark bars) was positively related with the outcome of an agonistic contest. Similar to *N. pulcher*, *N. caudopunctatus* winners showed body darkening more often than losers (Balzarini et al., 2017). Body darkening in this non-territorial context might have signalled agitation, or maybe even dominance. However, we could not find evidence that these bars reduced the costs (duration or intensity) of an agonistic conflict. Understanding the importance and significance of body darkening and baring in aggressive and other contexts is a avenue of future research that will shed light on this species' communication capabilities.

In summary, our results show that staged resource contests between single *N. caudopunctatus* were interactions of exceptionally low intensity. For example, closely related *T. temporalis* showed up to 60 aggressive bouts during a contest, while in an identical experimental set up *N. caudopunctatus* showed only 26 aggressive bouts per contest. Once paired, *N. caudopunctatus* showed more vigorous commensialistic defence, working with their neighbours to drive off territory intruders. While previous research on ecologically similar but socially different cichlids, revealed rapid and clear conflict resolution, *N. caudopunctatus*, as a semi-social cichlid that lives in dense aggregations with no hierarchical structure, showed a complex and restrained form of conflict resolution behaviour. Thus, our study contributes to the increasing knowledge of territoriality and conflict solving strategies and sets the stage for future studies on how these fish manage to co-exist in closely aggregated breeding territories and form colonies.

Acknowledgements

The first two authors contributed equally to this study. This study was financed by the Austrian Science Fund (FWF: standalone project FWF: P 27461). S.B. is supported by Natural Science and Engineering Research Council's Discovery and Accelerator grants. We are grateful to Martina Krakhofer, Bernhard Eckel and Ursula Madlsperger for help in maintaining the fish, and to Dr. Reddon and the reviewers for valuable input that greatly improved our manuscript.

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