Animal Cognition (2026) 29:11
https://doi.org/10.1007/s10071-025-02030-4

ORIGINAL PAPER

Stress in the spotlight: impacts of stress on learning and memory in a cichlid fish

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Received: 15 July 2025 / Revised: 28 November 2025 / Accepted: 28 November 2025

Abstract

Stress has been shown to both enhance and inhibit learning, which requires memory formation and memory retention. To date, the question of how stress influences learning and memory retention has been especially well studied in rodents and primates. Here, we expand our understanding of how stress influences memory formation and retention across vertebrates using the African cichlid fish, *Neolamprologus pulcher*. Fish were randomly assigned to either a control group or a stressed treatment group (with repeated chasing) and then trained to learn a foraging task, where they had to first learn to move a single disc off a food tray and then learned to lift a particular-coloured disc to receive the food reward. More unstressed (control) fish learned the final foraging task compared to the stressed fish although we did not detect a difference in the number of trials taken to reach the learning criteria or the number of mistakes between stressed and unstressed fish. Once the fish had learned the foraging task, we tested their memory for the task after 12, 24 and 48 days without reinforcement. We show that approximately 80% of the fish, regardless of treatment, remembered the task after 12 days, and 55% of the fish tested remembered even after 48 days. When we compared across all the memory trials, the stressed fish overall showed more memory compared to the control fish. Our results provide a memory decay curve and show that stress dampened learning while enhancing memory, thus expanding our understanding of fish cognition.

Keywords Fish cognition · Associative learning · Foraging task · Neural plasticity · Neolamprologus pulcher · Lake tanganyika

Introduction

Memory is the ability to encode, store, and later retrieve information and allows individuals to benefit from their experiences and thus increase their fitness (Ingraham et al. 2016). The benefits an individual gets from learning can depend on how good their memory is. Memory capacity varies between individuals, and is influenced by a host of factors, with stress playing a key role. Interestingly stress has been found to both enhance and impair memory (Joëls et al. 2006). Acute stress can amplify long-term memory formation in both humans and rodents (Goldfarb 2019) and has been shown to increase brain cell proliferation in rainbow trout (*Oncorhynchus mykiss*, Sørensen et al. 2013). However, the majority of studies indicate that stress, especially chronic stress, interrupts and inhibits both learning and memory (Trammell and Clore 2013; Schwabe and Wolf 2010; Sandi et al. 2005; Gaikwad et al. 2011). For example, stressed participants in a word recall study remembered far fewer items compared with unstressed control participants (Schwabe and Wolf 2010). Rats (*Rattus norvegicus*) that were exposed to cats performed much worse on a spatial memory task compared to control rats (Sandi et al. 2005) and predator-exposed zebrafish (*Danio rerio*) made more mistakes and spent less time in the target arm of a radial maze compared to unexposed controls (Gaikwad et al. 2011). Ramalingam and Madhaiyan (2023) found that zebrafish exposed to a predator had impaired short term memory in a spatial task and Pilehvar et al. (2020) found that copper exposure decreased associative learning in a T maze in this same species. Studies suggest that stressors can elongate the period needed to associate a learned cue with a

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reward, and that stressed animals can take longer to learn a task (Joëls et al. 2006; Koolhaas et al. 2011). Of course, the precise impact of stress on learning and memory depends on a myriad of factors such as the duration of exposure, the age, sex, and reproductive status of the exposed individual and the way learning and memory are probed (Ramalingam and Madhaiyan 2023; Schwabe et al. 2012; Vogel and Schwabe 2016**).**

In this study, we set out to explore the impacts of stress, and more specifically to examine how an acute stressor influences learning and memory retention. We used the group living cichlid fish, *Neolamprologus pulcher*, to address both our research aims. *N. pulcher* is a freshwater cooperative breeding, group living, cichlid fish species from Lake Tanganyika (Wong and Balshine 2010). In *N. pulcher* the two largest, most dominant individuals in each social group are a reproductive pair that are helped by subordinates in territory defense, territory maintenance, and in raising offspring (Stiver et al. 2005; Wong and Balshine 2010). We used a foraging based learning task because previous work illustrated that this fish species readily learns to lift small discs off a welled tray to receive a food reward (Stanbrook et al. 2020; Culbert et al. 2020, 2021a; Fischer et al. 2021; Guadagno and Triki 2024; La Loggia et al. 2022; Latchem et al. 2025; Reyes-Contreras and Taborsky 2022). *N. pulcher* are capable of learning this task quickly, reaching the learning criterion after ~ 19 trials if learning on their own and after ~ 15 trials if they learn the task from others (Latchem et al. 2025). Moving discs out of the way to get access to food rewards uses the same behavioural actions observed in wild *N. pulcher* as these fish regularly use their mouths to move and carry sand, stones and snails away from their territories and shelters (Heg and Taborsky 2010). Although in the wild adult *N. pulcher* mainly feed on planktonic zooplankton (Balshine et al. 2001; Wong and Balshine 2010), young *N. pulcher* mostly feed on zooplankton gleaned from the substrate and even adults occasionally eat off the substrate (S. Balshine pers obs).

Researchers have used a variety of methods to induce stress, such as restraint, social isolation, exposure to a predator cue or contaminants, heat and air exposure (Demin et al. 2020; Bali and Jaggi 2015; Iwama et al. 1998). We selected to chase our fish because chasing is a practical repeatable method that reliably generates stress and has been used in many previous studies, including one on a related fish species, *Amatitlania nigrofasciata* (Moscicki and Hurd 2015). A number of previous studies have found a link between dominance rank and cortisol levels (an indicator of stress) in *N. pulcher* (Bender et al. 2006; Mileva et al. 2009; Ligocki et al. 2019; Culbert et al. 2021a, b). For example, Mileva et al. (2009) discovered that dominant fish, who regularly police subordinates, had higher baseline cortisol compared to subordinates. Culbert et al. (2021b) also found that dominants had a higher level of cortisol compared to subordinates in a study of a wild population of *N. pulcher* in Lake Tanganyika (this study used a non-invasive scale cortisol measure). In contrast, Bender et al. (2006), using a non-invasive holding water cortisol assay, found no difference in cortisol levels between subordinate and dominant males. To avoid any possible rank-based difference in baseline stress levels, in this study, we opted to only use dominant *N. pulcher*.

In addition to social rank, sex can also impact stress levels (Bale and Epperson 2015; Campbell et al. 2021; Jonasson 2005; Rambo et al. 2017). Males and females can be exposed naturally to different levels and types of stress and may experience and respond to stress differently (Wendelaar Bonga 1997). For example, chased female convict cichlids decreased their freezing time, but this was not true of chased males (Moscicki and Hurd 2015), and stressed female zebrafish, but not males, increased locomotion (Rambo et al. 2017). In *N. pulcher*, chased females had slower growth, and longer spawn intervals compared to unstressed females; with males not showing these patterns (Mileva et al. 2011). Sex can also have an impact on cognition, as memory and learning capacity commonly differs between males and females. Males in a number of studies have been shown to have superior spatial learning and to sometimes learn faster (Lucon-Xiccato and Bisazza 2017; Newhouse et al. 2007) while females often have better social learning capacity and higher cognitive flexibility (Lucon-Xiccato and Bisazza 2014, 2017). There are also a number of studies where no sex differences in memory and learning were found (Lucon-Xiccato and Dadda 2016; Lucon-Xiccato and Bisazza 2014, 2017). In this study we used both male and female *N. pulcher* to examine how stress influences learning and memory.

Learning and memory have been well studied in fish (Brown and Laland 2003; Gerlai 2011, 2017; Lucon-Xiccato and Bisazza 2014, 2017; Lindeyer and Reader 2010; Rodríguez, et al., 2002; Salas et al. 2006). As with other animals, fish continually interact with their surroundings, taking information in through their sensory systems and then use learning and memory to interpret and apply this sensory input (Fernö et al. 2020). Learning and memory are generally considered to be most useful in changing environments (Dunlap et al. 2019). For example, in areas where disturbances are common, the rapidly changing environment can cause stress but also be the context in which learning and memory are most strongly selected for (Wong and Candolin 2015). While fish lack a hippocampus (a specialized brain region for forming memories found in humans), they have an analogous brain region called the lateral pallium, which is also thought to be used for long-term memory retention (Rodríguez et al. 2002). Many fish species have been shown to have long-term memories that last anywhere from 24 h to several months (Reebs 2008). For example, zebrafish can recall which side of a tank will result in a food reward after a 10-day period without any reinforcement (Williams et al. 2002) while the gobiid fish, *Bathygobius soporator*, can retain memories for 40 days (Aronson 1971), the paradise fish, *Macropodus opercularis*, for 3 months (Csányi et al. 1989), and wild bluestreak cleaner fish, *Labroides dimidiatus*, for 11 months (Triki and Bshary 2019). The longest previous memory test attempted with a cichlid fish was with *Labidochromis caeruleus*, which could retain a preference for a reinforced visual cue for a 12-day period (Ingraham et al. 2016). By investigating how long *N. pulcher* might retain an association between a particular coloured disc and a food reward, we aimed to extend our knowledge of fish cognition.

We tested *N. pulcher* using an experimental learning protocol previously designed for guppies (Lucon-Xiccato and Bisazza 2014; Buechel et al. 2018) and a memory protocol that was based on Ingraham et al. (2016) memory study on the related African cichlid, *Labidochromis caeruleus*. Finally, given that bold, active, and more exploratory individuals often take more risks, have higher resilience to stress (Moscicki and Hurd 2015), and may have more opportunities to learn (Griffin et al. 2015), we also conducted behavioural assays (boldness, exploration and activity) prior to the learning trials. These behavioural trials were used to assess whether an individual's boldness, exploration and activity levels might be related to their learning speed or memory. Hence our aims were threefold: (1) to further explore the role of stress on learning and memory retention in fish (2) to conduct the first memory test in the group living species *N. pulcher* while expanding the memory timeline for cichlid fishes and (3) to examine the links between behaviour, learning and memory. We predicted that stress, as in many other species, would slow down learning and cause worse performance on the memory tests compared to the unstressed controls. Since *N. pulcher* live in permanent social groups with well-established social ranks (Stiver et al. 2005), with segregated individual sub territories (Werner et al. 2003), and individual recognition (Le Vin et al. 2010), all tasks that require memory, we predicted that this species would be able to remember how to find a food reward for longer than 12 days. Finally, we predicted that bolder, more active, and exploratory individuals would learn faster because they would take more risks and have more opportunities to learn.

Methods

Study animals and housing conditions

This study was conducted at the Aquatic Behavioural Ecology Laboratory at McMaster University between June 2024 and January 2025 using laboratory-reared male and female dominant *N. pulcher*. Prior to the experimental trials, the fish had been held in 189 L social tanks lined with 5 cm of coral sand substrate in groups of two to four fish. These social aquaria were held at 26 to 28˚C, and on a 12:12 h light: dark cycle. The tanks contained a sponge filter and clay flowerpots that were used as shelter. Fish were fed until satiation six days a week with commercial fish flakes (Nutrafinbasix) and bloodworm one day a week. Every fish used was measured for their standard body length (in 0.1 cm), body mass (to the nearest 0.01 g), sexed, and individually tagged.

Learning assay

The learning assay used in these experiments involved teaching fish to move plastic discs (2 cm in diameter) off of a feeding tray (a white rectangular plastic block 2 × 10 × 5 m, with 10 evenly spaced 0.9 × 0.5 cm wells on top) to access a food reward in one of the wells, following methodology developed for guppies (Lucon-Xiccato and Bisazza 2014) and well tested in *N. pulcher* (Culbert et al. 2020, 2021a; Fischer et al. 2021; Guadagno and Triki 2024; La Loggia et al. 2022; Latchem et al. 2025; Stanbrook et al. 2020).

Experimental learning tanks

The learning tanks were 70-liter aquariums (length of 76 cm x width of 30.5 cm x height of 30.5 cm) separated into three sections. Each tank had two outer sections of equivalent size and a larger central compartment (Fig. 1a). The compartments were separated from each other by an opaque movable plastic barrier, that blocked fish in one section from seeing into the other sections. The learning tanks were maintained between 26 and 28˚C and on a 12:12 h light: dark cycle, contained 2 cm of coral sand substrate, an air stone, a mechanical filter, and each outer compartment contained a half clay pot. The central section was where the learning assay was conducted (by placing the feeding tray with food covered by plastic discs). Fish were randomly assigned to either the stressed treatment group (N=24) or an unstressed control group (N=23). We initially had equal numbers of stressed and unstressed fish, but there was one age related mortality in the control group leading to slightly different group sizes. Although we attempted to test an equal number of males

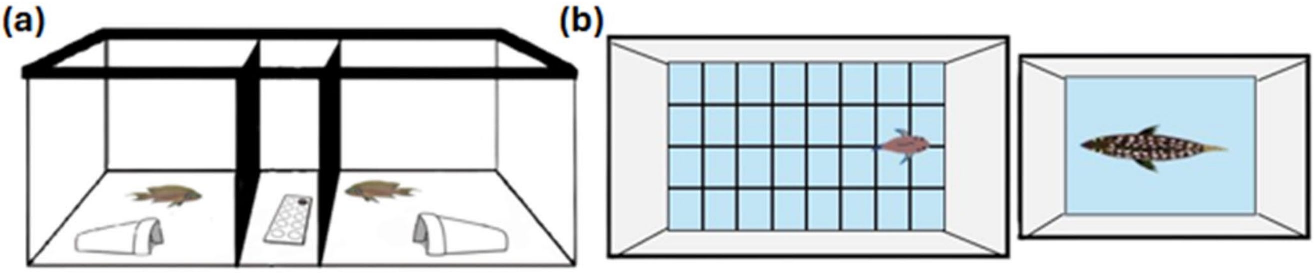

Fig. 1 The experimental tanks used. (**a**) A side view of the learning trial tank, showing the tank separated into three compartments, with an individual fish and a shelter in each outer compartment and the food tray in the center. Taken from Latchem 2025. (**b**) A top view of the boldness and exploration/activity behavioural tank, showing the grids in the large tank and the predator fish beside the *N. pulcher* in a separate tank

(*N*=22) and females (*N*=25), we ended up having slightly more females. The mass of the fish used ranged from 2 g to 12 g. Fish in the unstressed control group were always placed into one of the outer compartments in a learning tank (chosen at random) and given 24 h to acclimatize before they started their learning trials. Fish in the stressed group were placed into an outer compartment of the learning tank and within an hour the learning trials would start.

Stress procedure

All fish in the stress group were stressed daily, immediately before their first learning trial. Fish were stressed following the chase procedure described in Moscicki and Hurd (2015). First, the half clay pot was removed from their end section of the tank, and then the handle of a small dip net was placed into the water. The net handle was then moved in a figure eight pattern for two minutes. If the fish stopped moving during this two-minute chase, we would wait 10 s and then resume moving the net in a figure eight pattern. After this two-minute chase, the shelter was returned, providing the fish a place to hide, and the learning trials began immediately. As mentioned above, the fish were only chased prior to the first learning trial on each day. This meant that the stressor could be applied for a minimum of two days (one day for the initial single disc trials, and one day for the two disc trials) and up to a maximum of 17 days (nine days of the single disc trials and eight days for the two disc trials, see below).

Phase 1: initial associative (single disc) learning trials

Prior to the start of the learning trials, all fish were given one hour to individually explore the central compartment and feeding tray in their learning tanks. During this exploration period there were no discs on the feeding tray nor was there any food in the wells. After the fish in the stressed group had been chased and all fish had explored the central compartment, we started the learning trials.

During the single disc learning trials, a piece of blood worm was placed into a random feeding well, and a green plastic disc (diameter of 2 cm) was placed near that well. After the fish were familiar with the learning apparatus and were consistently eating the blood worm, the green disc would be placed so it covered a part of the well. After each successful reward retrieval trial, more of the well would be covered by the disc, until eventually the disc completely covered the well and the fish was forced to move the disc to be able consume a food reward. We conducted 10 trials per fish per day for a total of nine days. Once the fish learned to move the disc to receive a food reward (i.e. they moved a disc that fully covered the well three times in a row), we would move this individual onto the next phase of the experiment, called the discrimination two-disc learning trials. After the completion of all learning trials, fish were fed until satiation with commercial food flakes.

Phase 2: discrimination (two-disc) learning trials

Once fish were consistently moving the disc (ie. moved the disc from a fully covered well three times in a row), we began the discrimination learning trial phase. All housing conditions and tank sizes were the same as in the training trials described above. In the discrimination learning trials, fish were faced with a feeding tray with not one but two discs on it; one disc was black, and the other was red. Both discs were placed on the feeding tray fully covering wells with a food reward (a bloodworm) underneath them. For each fish, one disc colour was the correct one and simple to move while the other colour was ‘incorrect’. The incorrect disc was extremely difficult to remove as there was a bolt attached to the disc’s underside, which was both heavy and fit snugly into the well on the feeding tray. Half of the fish learned that it was possible to move a black disc, while the other half learned that it was possible to move a red disc. We ran 10 discrimination trials a day for a maximum of eight days (10 consecutive trials per day with each trial lasting for 2 minutes). Once a fish learned to move the correct coloured disc (i.e. got it right in 8/10 trials), it was deemed ready for their memory tests. We selected the learning criterion to consist of eight correct choices out of 10 trials based on the methodology developed by Lucon-Xiccato and Bisazza (2014). Only fish that learned (lifted the correct disc in 8/10 trials) were allowed to go forward and onto the memory phase. The same day that they learned, the fish were taken back to their social housing tanks (see above) starting a 12-day rest period (with Day 1 being the day after they finished learning the discrimination task and managed to get the right disc colour moved in 8 out 10 trials). To avoid food neophobia, once a week bloodworms (that were used as a reward in the foraging assays) were fed to the cichlids in their social housing tanks.

In our experiment, we used green (for the single disc learning trials), black, and red discs (for the two-disc discrimination trials). These are all colours that *N. pulcher* would naturally interact with as they have red dots on their bodies, black opercular marks on their faces, and green eggs. These colors have also been used in previous learning studies (Culbert et al. 2020). The chromatic contrast and achromatic contrasts between red, green, and black are well above the 'just noticeable difference' (JND) threshold for colour discrimination (Culbert et al. 2020; van den Berg 2019), suggesting that green, red, and black are easily distinguishable colours for *N. pulcher* (Barnett et al. 2023).

Phase 3: memory tests/probe

We ran our memory tests at specific time intervals (12, 24, 48 and 96 days) after the fish successfully completed their discrimination learning trials (i.e. they reached the learning criterion). For the memory tests, fish were moved from their social housing tanks to the same learning tank where the original learning trials took place. Both the control and the stressed fish were given a 24-hour acclimatization period following transport to their learning tank prior to their memory tests. The first memory test probe consisted of a black and a red disc on a tray just as the fish experienced in the discrimination learning trials, but in this memory test neither disc was bolted in and no food reward was provided under either disc. Fish were given up to three 5-minute trials to remember the "correct" disc (the disc colour they had learned to move in the 2 disc discrimination learning trials). If the fish lifted or moved the correct disc once within the three possible trials, then we deemed this fish as having a memory of how to do the task. If the fish moved the correct disc on their first memory trial, they did not have a second or a third trial. If the fish did not interact with the discs over three trials or lifted the wrong disc, they were considered to have failed the memory task. If a fish failed the memory task, they were immediately returned to their housing tanks and did not continue in the experiment.

Given that no food reward was given for lifting the correctly coloured disc in the memory probe test, we needed to ensure that these memory tests did not cloud the fish's recall in the future, so we ran a few reinforcement trials. When a fish remembered on their first trial, they were given three 2-minute reinforcement trials right after their memory probe test, using the same methods as the discrimination learning trials, where one disc colour was correct and possible to move while the other disc colour was incorrect and impossible to move. If the fish remembered on the second trial, they were given six 2-minute reinforcement trials right after their probe test, and if the fish remembered on the third trial, they were given nine 2-minute reinforcement trials. After the reinforcement trials, the fish were moved back into their social housing tanks until the next memory test took place. The treatment fish (stressed group) were not stressed again, before the memory probe nor during any of the reinforcement trials. So, the stress was associated only with the learning phase and not with the memory test.

As mentioned above, the memory or probe test was conducted 12, 24, 48, and 96 days after each respective fish had learned the discrimination task. There was one exception where a fish was accidentally tested on Day 25 instead of Day 24. Note that only fish that remembered proceeded to the next stage in the memory timeline, in other words fish that remembered at Day 12 were tested on Day 24, and only fish that remembered on Day 24 were tested on Day 48 and so on. While we established the memory days to reflect how many days had passed since the fish learned the discrimination task, we consider the fishes *memory retention* period to be 12 days, 24 days, and 48 days due to the reinforcement trials we conducted. Thus, the maximum number of days a fish could remember in our experiment was 48 days. All learning trials and the memory tests were filmed from the side using a Sony FDR-AX700 Handycam set up 1 m in front of the tanks.

Behavioural assays

To explore if behaviour influenced learning and/or memory, activity, exploration, and boldness tests were conducted on all fish prior to running the learning trials. To conduct these tests, fish were placed into a transparent tube (with a diameter of 11.4 cm and a height of 32 cm) inside a large glass tank (91.4 cm x 45.7 cm x 43.2 cm) for five minutes. The floor of this behavioural assay tank had a grid marked

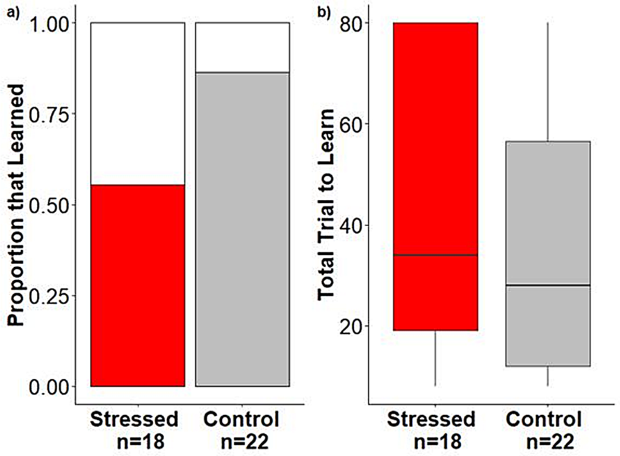

Fig. 2 The effects of stress on learning in *Neolamprologus pulcher*. (**a**) A bar plot showing the proportion of fish that learned the discrimination learning task with red representing stressed fish and grey representing control fish. (**b**) A box plot showing the number of trials it took fish to learn to move the correct disc in the discrimination learning trials. The top and bottom of the boxes represent the third and first quartiles, the bold bars represent the median, and the boxes represent the interquartile range

Table 1 Behavioural assay variables used in the factor analysis for behavioural trials

Variable	FA1	FA2	FA3	Communality (h^2)
Inside the Arena (in seconds)	0.02	0.05	0.50	0.20
Time Near Predator (in seconds)	0.23	**0.70**	0.02	0.46
Unique Grids Crossed	**0.76**	−0.19	0.21	0.73
Total Grids Crossed	**0.76**	0.19	−0.21	0.72

The two behavioural variables that loaded highly on Factor 1 (FA1) are the number of unique grids crossed (out of 32), and the total number of grids crossed. The behavioural variable that loaded highly on Factor 2 (FA2) was the time the fish spent near the predator. We present Factor 3 (FA3) here as it had the strongest loading of time spent in the center of the tank (the inner grid squares), but this factor was not included in our analysis. Communality represents the proportion of each variable explained by the factors

on it with 10.8 cm x 10.8 cm squares. The clear tube was removed remotely using a pulley system, and each fish was given 10 min to swim freely around the tank. After the first 10 min, an opaque barrier on one side of the tank was lifted, revealing another neighbouring tank containing a predator cichlid (*Lepidiolamprologus kendalli*), from Lake Tanganyika. We measured how willing each fish was to be close to the predator for 5 min (Fig. 1b). Our methodology for these behavioural tests was based on Latchem et al. (2025) and Schnörr et al. (2012). Each 15-minute trial was filmed from above using a Sony FDR-AX700 Handycam.

Scoring behaviour

All the videos were scored using Behavioural Research Interactive Software (BORIS, version 8.25, Friard and Gamba 2016). Six research assistants helped score the 1,600 + videos; all were blind to the treatment group that the fish came from. For each two-disc discrimination trial, we scored the time taken by the focal fish to move the correct disc, the time the fish spent in the center (riskier) area of the tank, and the number of times the fish interacted with the incorrect disc (mistakes). We considered the fish to be in the tank's center section if at least three-quarters of its body was in that section. We considered the fish to have made a mistake any time the fish touched or tried to move the bolted, 'incorrect', disc. Although mistakes were analyzed, they were not used as our main criteria of learning or memory. Instead, lifting of the correct disc and getting the food reward was our threshold for learning; mistakes likely to extend the time until the learning threshold is reached. In the behavioural trials, the total number of gridlines crossed during the 15-minute trial was used as a measure of activity. The number of "unique" grid lines crossed in the first 10 min was also recorded and was used as a measure of exploration. Boldness was determined by calculating the time (in seconds) fish spent in the squares in the center of the tank and away from walls. To quantify risk propensity, we measured time (in seconds) that each fish spent near (four closest squares) the predator in the last 5 min of the trial while the predator was visible.

Statistical analyses

All analyses were performed using R version 4.2.2 (R Core Team 2021). We tested for normality and equality of variances using the Shapiro-Wilk test. If the data was not normally distributed, we attempted to normalize it with transformation, but if those transformations did not result in normalizing the data, we employed non-parametric tests.

The results of the behavioural tests were highly correlated with each other (Fig. 2). Thus, to reduce the number of statistical tests that had to be run, we conducted a factor analysis (psych package in R) on the measures of activity (total grid lines crossed), exploration (number of unique grid lines crossed), and boldness (time spent in the center, and the time near the predator). After performing the factor analysis, we determined that it would be appropriate to include the first two factors as they explained 72.5% of the variance (Table 1). These two factors were used to analyze if the behavioral measurements impacted the likelihood of individuals learning the foraging task, or the number of trials it took individuals to learn the task. Factor one (FA1) represented activity as the number of grid squares and the number of unique squares loaded strongest on this factor. Exploration (number of unique grid squares) and activity (number of total grids crossed) were correlated ($r=0.43$). Factor 2 (FA2) was deemed to represent boldness as time spent near predator loaded strongly on to this factor. Time spent in the middle of the grid and the time spent near the predator were negatively correlated ($r=-0.27$).

One fish was excluded from the factor analysis because their behavioural trial video was corrupted. Seven fish failed to learn the single disc learning task and thus were excluded from the two-disc discrimination learning trials. From this point onward, any reference to a learning or the foraging task refers to the two-disc discrimination trials only.

We used generalized linear mixed-effects models with a binomial error structure (dyplr package in R) to examine if stress or sex influenced the ability of fish to learn the discrimination task. A fish that successfully reached our learning criterion (8/10 correct trials) was coded as a “1”, while fish that failed to reach this criterion was coded as a “0”. We built two separate models, one with stress and one with sex as the response variable. In each model we also included the standard length (in mm), the disc colour the fish learned to move, as well as the two factors (F1 and F2) from our factor analysis into our models as random effects. In both models, we included the unique ID of each fish as a fixed effect. We then used the Dredge function in R (R package *MuMIn*) to determine the model of best fit. The dredge function calculates the AIC corrected (AICc) scores of all possible models. We chose the model of best fit that included our principal response variable (treatment or sex), with an improvement in the AICc scores of at least 2 being deemed as a better fitting model. We found that the model of best fit included only the principal response variable. We used likelihood ratio tests to test statistical significance of terms in both models. We then tested if stress or sex affected the number of trials it took to learn by running Wilcoxon- rank sum tests. Any fish that failed to learn to move the disc was given the maximum number of trials (80).

The influence of stress on memory was tested both across all memory trials and separately for each memory trial. We tested for differences between groups across all trials by using a permutation-based chi-squared test, using the number of fish that failed in each memory test to avoid repeated measures. We also ran a chi-squared test with yates’ correction to compare the performance of each group on each memory test day. In addition, we tested if an individual’s behaviour influenced learning by checking the correlations between FA1, FA2, and the number of trials it took to learn for both the stressed and control fish. To do this, we employed a Pearson correlation test when the data was normal and a Spearman correlation for non-normal data. We also investigated if there were any behavioural differences between stressed and control fish in terms of the amount of time spent in the center compartment, and the number of mistakes made using independent t-tests and Wilcoxon Rank Sum tests (if the data was not normal and could not be transformed).

Results

Learning in stressed vs. control fish

We found that 86% of the control fish (19 out of 22) and 56% of the stressed fish (10 out of 18) successfully learned the discrimination foraging task with stressed fish being significantly less likely to learn to move the correct disc (GLMM, $X^2=4.3$, df=1, $p=0.04$, Fig. 2a). Stressed fish took 34±9 trials (median±SE) to learn while unstressed fish took 28±7 trials, but this difference in number of trials to learn did not reach significance (Wilcoxon rank test, W=247, $p=0.18$, Fig. 2b). No sex differences were found in the likelihood of learning, with 77% of males (17 out of 22) and 92% of the females (23 out of 25) learning successfully (GLMM, $X^2=0.23$, df=1, $p=0.63$, Fig. 3a.). Males and females also took a similar number of trials to learn (Wilcoxon rank test, W=161.5, $p=0.35$ Fig. 3b).

Memory and stress

Memory for the foraging task was tested after 12, 24, and 48 days without reinforcement. Of the fish that successfully reached our learning criterion, 79% (or 23 out of 29) successfully remembered the task after a 12-day break from training. We found that 90% of the stressed fish (or 9 out of 10) remembered, and 74% (or 14 out of 19) of the control fish remembered after this 12 day break (Fig. 4a). Our second memory test (on Day 24) represented 12 days since the last reinforcement trial, and 24 days since the learning criteria had been reached. On our day 24 test we found that only 65% (or 15 of the 23) fish remembered; 78% (or 7 out of 9) of the stressed fish remembered and 64% (or 8 out of 14) of the control fish remembered. By the third memory test (Day 48) the fish had not been reinforced for 24 days, 73% (11 of the 15) of the fish tested; with 100% (or 7 out of 7) of the stressed fish and 50% (or 4 out of 8) of control fish remembering. Finally, on the fourth and last memory test (on Day 96), the fish had not been reinforced for 48 days, we found that only 55% of the fish tested remembered ($n=6$); 57% (or 4 out of 7) of stressed fish and 50% (or 2 out of 4) of the remaining control fish. We did not find that there was a significant difference in memory between the stressed and control groups on any of the individual memory tests days (i.e. Day 12, 24, or 48, See Table 2; Fig. 4b and c). However, when we compared the performances of the two groups across all memory tests, we found that more control

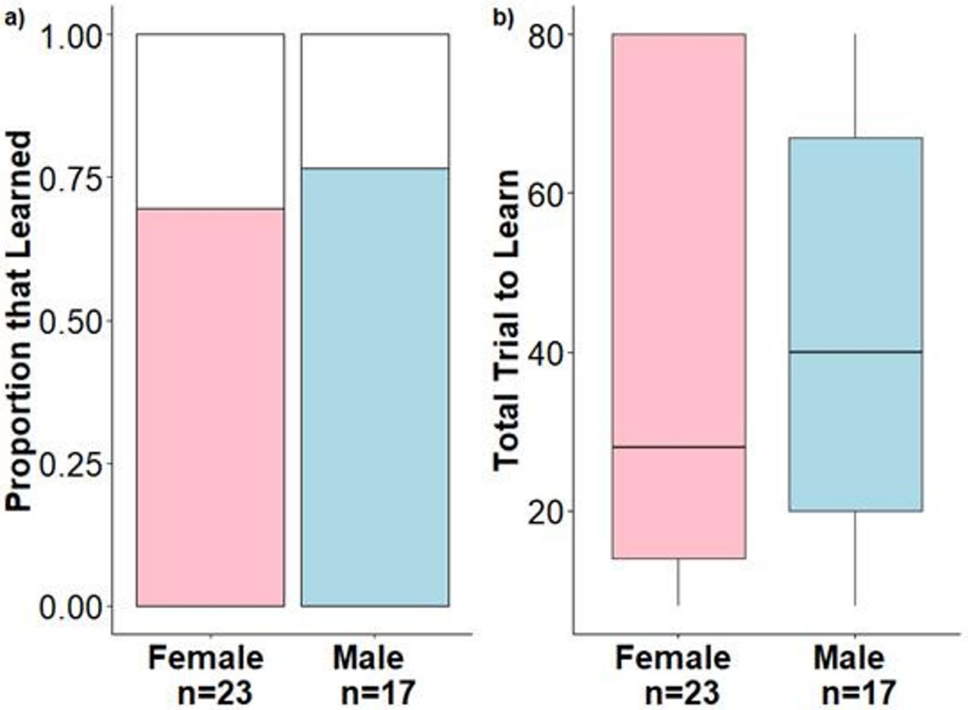

Fig. 3 The effects of sex on learning in *Neolamprologus pulcher*. (**a**) A bar plot showing the number of fish that learned the discrimination learning task with pink representing female fish and light blue representing male fish. (**b**) A box plot showing the number of trials it took fish to learn to move the correct disc in the discrimination learning trials based on sex. The top and bottom of the boxes represent the third and first quartiles, the bold bars represent the median, and the boxes represent the interquartile range

fish failed to remember the task (*V*=0.54, chi-squared test, X^2 = 8.23, df=1, *p*=0.04).

Memory and sex

No sex differences were found the on the first three memory test days (i.e. on Day 12, *V*=0.032, chi-squared test, X^2=0.031, df=1, *p*=0.86; on Day 24, *V*=0.06, chi-squared test, X^2=0.08, df=1, *p*=0.78; or on Day 48, *V*=7×10^{-17}, chi-squared test, X^2=7×10^{-32}, df=1, *p*=1). However, more females than males remembered on Day 96 (*V*=0.65, chi-squared test, X^2=4.65, df=1, *p*=0.03, Fig. 5).

Behaviour of stressed vs. control fish and links to learning

During the foraging learning trials unstressed control fish spent more time in the riskier center of the arena (median=99.4±4.2 s) compared to stressed fish (median=78.4±6.3 s, Wilcoxon rank-sum test, *W*=82, *p*=0.001). However, control and stressed fish made the same number of mistakes with respect to touching the wrong disc (control median=0.8±0.2, stressed median=1.3±0.2, Wilcoxon rank-sum test, *W*=238, *p*=0.28). During the behavioural trials neither fish activity (FA1) nor boldness (FA2) correlated with how many trials fish took to learn (FA1, *r* = −0.24, *t* = −1.49, df=37, *p*=0.15 or FA2, *r* =- 0.02, *t* = −0.01, df=37, *p*=0.98). Relationships between the factor analysis of the behaviours and the number of trials it took fish to learn were also analyzed separately for the stressed and control groups, as stress can influence the behaviours measured. We did not find a correlation between how quickly the stressed fish learned and either their FA1 (*r* = −0.25, t = −1.04, df=16, *p*=0.32) or FA2 scores (*r*=0.15, t=0.63, df=16, *p*=0.53). We similarly did not find any correlations between FA1 and learning (*r* = −0.09, t = −0.40, df=19, *p*=0.69) or FA2 and learning (*r* = −0.13, t =- 0.59, df=19, *p*=0.56) in the unstressed fish in the control group.

Discussion

In this experiment we tested how stress and sex influenced the learning and memory capabilities of the social cichlid, *Neolamprologus pulcher*. Stressed fish were less likely to learn how to complete the foraging task, suggesting that stress impedes learning in this species, however, stress appeared to improve memory capacity with *N. pulcher*; with more stressed fish remembering and some fish able to remember the previously learned foraging task for up to for 48 days with no additional reinforcement. Males and females did not differ in learning, but females had better memory capacity after 48 days. Fish behaviour (activity, exploration, and boldness) was not correlated to learning probability or speed, nor did these behaviours correlate with memory capacity.

Stress has been shown to reduce the learning capabilities in other species, including many fish species, such as

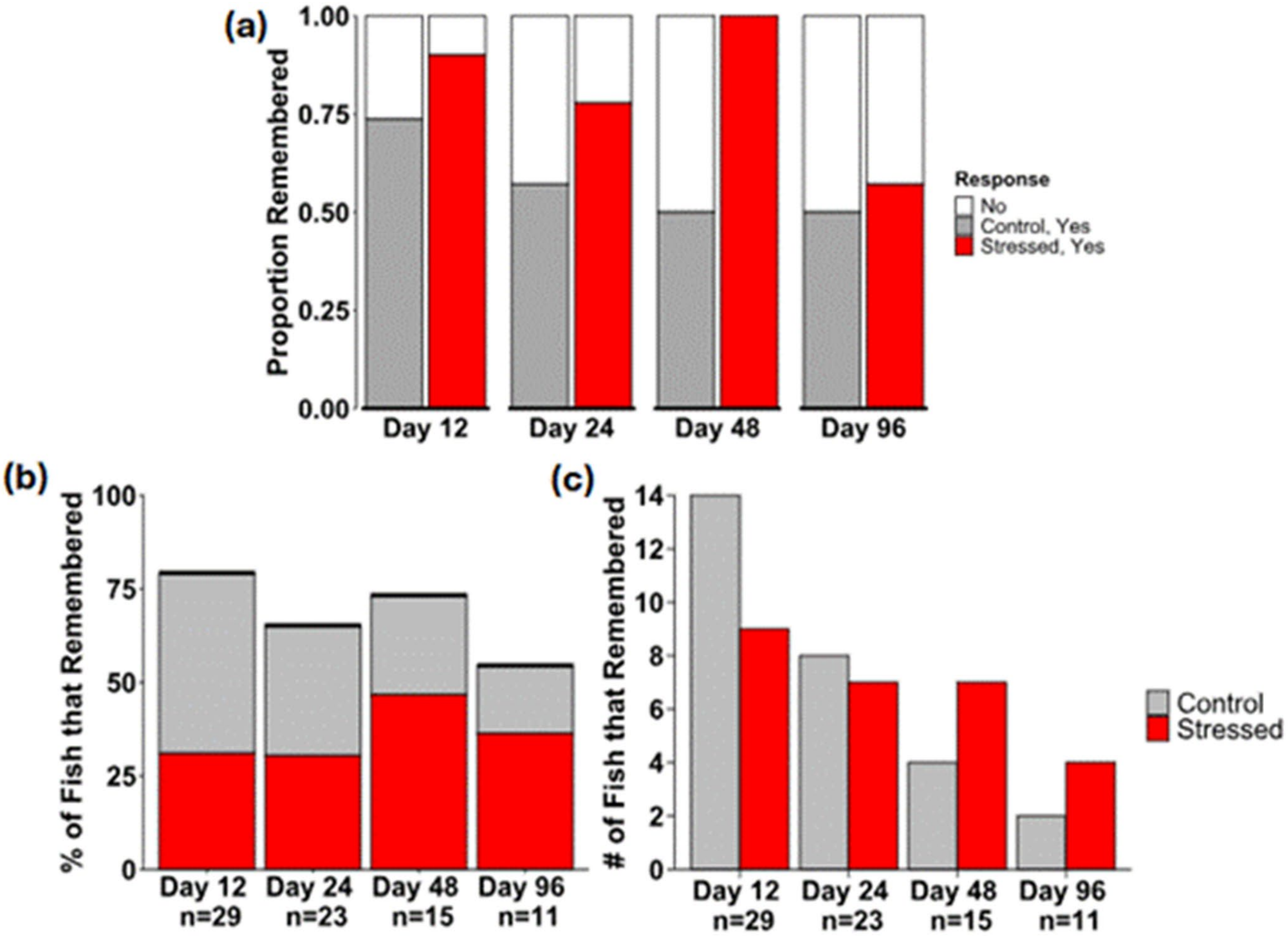

Fig. 4 The effects of stress on memory across the different days that the memory tests were applied. (**a**) A double bar plot showing the proportion of the total fish tested, either from the stressed or control groups, who remembered on day 12, 24, 48, or 96 of their memory test. (**b**) A stacked bar plot comparing the difference in the percentage of stressed (in red) and control groups (in grey) that showed memory retention on each memory test day. (**c**) A double bar plot showing the drop in the raw count of the stress and control fish that retained the ability to do the foraging task on each of the memory test days

Table 2 Results from chi-squared and cramer's *V* tests showing the number of fish tested across the four different memory test durations

Memory Day	Number of Stressed Fish that Remembered	Number of Control Fish that Remembered	*V*	X^2	df	*p*
Day 12	9 (of 10)	14 (of 19)	0.10	0.30	1	0.58
Day 24	7 (of 9)	8 (of 14)	0.12	0.32	1	0.57
Day 48	7 (of 7)	4 (of 8)	0.41	2.56	1	0.11
Day 96	4 (of 7)	2 (of 4)	5×10^{-17}	3×10^{-32}	1	1

V represents effect size values for the Chi-squared tests (X^2), *Df* are the degrees of freedom, and *p*-values represent the significance levels. The number of fish that successfully remembered is represented by the first number, and the total number of fish in each group that were tested each day is represented by the brackets

zebrafish (Gaikwad et al. 2011; Baker and Wong 2019). A common response to stress in fish is reduced activity, either by freezing or seeking cover (Galhardo and Oliveira 2009). In our experimental setup, the learning apparatus was located in the center of our learning tanks, requiring the fish to swim away from their shelters into an open area to interact with the tray with the food reward. We found that the stressed fish in our study spent significantly less time near the learning apparatus during learning trials compared with the control unstressed fish. Fish with low motivation to interact with a learning apparatus would be less likely to learn (Wood et al. 2011). Increased stress can also suppress appetite in fishes (Conde-Sieira et al. 2018), as has been documented in the European seabass *Dicentrarchus labrax* (Leal et al. 2011). It is possible that a food reward was not as appealing to the stressed *N. pulcher*, which may have also dampened their motivation to learn. In this experiment, we also only tested individual learning, which is typically a harder and higher

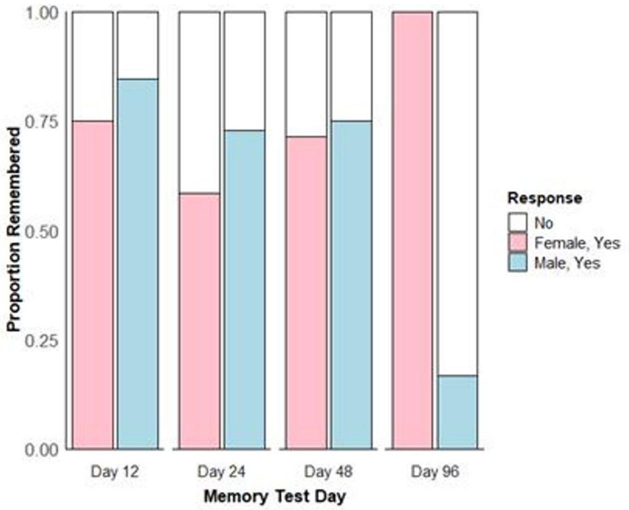

Fig. 5 The effect of sex on memory in *N. pulcher*. A stacked bar plot showing the proportion of fish that remembered on each test day. Females are represented by pink while males are represented by light blue. The only sex difference observed was on Day 96

risk way to learn than some alternative methods, such as social learning (Kendal et al. 2005; Latchem et al. 2025). Future research could consider different learning rewards or different ways of learning to better understand the full impacts of stress.

While there was no significant difference between the performance of the stressed or control fish on any particular memory test day, when we examined the data across all the memory trials, we found that the stressed fish were more likely to remember. In our study, we applied a daily but short-term stressor (chasing) and did so for just two minutes. It is possible that a more chronic or more severe stressor (such as air exposure) would have had an even stronger negative impact on learning and memory. It has been found that chronic stress can cause hippocampal atrophy in humans and can decrease the number of neurons in the hippocampus (Kim et al. 2015). Stressful events may increase the saliency of events associated with the learning paradigm and therefore be remembered better (Joëls et al. 2006). It has been found that increasing levels of stress hormones at the same time and in the same context of the task being learnt can lead to better memory retention (Joëls et al. 2006). The opposite is true when the stressor is applied before or after the learning task, with exposure to stress before a learning task impeding the declarative memory of humans (Kirschbaum et al. 1996). Our fish experienced the acute stressor (chasing) in the same tank as their foraging learning task and in the same location that we later tested their memory in, however, the fish received the stressor an hour before their memory test. Also, our fish were chased with a net, which may or may not be a generalizable stressor to real-world predation situations. To more comprehensively understand how a temporal pairing between the learning task and the presentation of the stressor impacts memory more research is now needed that explores the impact of chronic stress and on the severity of stressor on learning or memory.

We found that *N. pulcher* were able to remember the foraging task for a much longer period than is typically tested in memory experiments for fishes. As expected, fewer and fewer fish were able to remember as the duration between memory testing increased. Most studies examining fish memory have done so on shorter time scales of 12 days or less (Ingraham et al. 2016) but our findings suggest that 12 days may not be sufficiently long to determine the impacts of acute stress on memory retention. Based on our experiment, the maximum length of memory retention for *N. pulcher* appeared to be 48 days. It is of course possible that this species, *N. pulcher*, can remember for even longer. It is worth mentioning that the only 'true' memory test day in our study occurred on Day 12, as the fish did not encounter the learning stimulus during their rest period. We gave reinforcement trials ($n = 3$ to 9) to each fish that successfully completed the memory test. We did this to ensure that their memory test experience of lifting the correct colour without receiving a reward, did not extinguish the fish's associated colour contingency rule. Our design of repeatedly testing the same fish at different intervals was necessitated by the limited number of available fish in our laboratory.

Based on an extremely small sample, it appears that female *N. pulcher* could have better memory compared to males at Day 96. Why might this be? Female *N. pulcher* are philopatric while males disperse to new territories to breed and often hold more than one territory (Dierkes et al. 2005; Stiver et al. 2006; Schürch and Heg 2010; Wong and Balshine 2010). Hence, while females might benefit from knowing the spatial layout and the details of what areas in their territory are the best for feeding, for males, who disperse and move more between territories, holding on to such knowledge may not be as advantageous. However, we would then expect females to learn faster as well, and we did not see sex differences in learning speed. In some fish, males and females differ in ways that lead us to expect cognitive sex differences (Lucon-Xiccato and Bisazza 2017). For example, female guppies, *Poecilia reticulata*, can differentiate the intensity of colour spots and notice differences in shape and size better than males (Houde 2019). Even after one encounter, female guppies can memorize a male's features (Eakley and Houde 2004) and this makes sense given that male guppies are exquisitely unique in their colour patterns, but females are not. However, in other fish species like the rainbowfish, *Melanotaenia duboulayi*, males and females did not differ in their learning rate when learning a colour association task (Bibost and Brown 2014). Fontana et al. (2019) did not find any sex differences in learning or memory in zebrafish, but they only looked at ‘short-term’ memory of spatial tasks. A previous study in our laboratory used a similar foraging task to study how social rank influenced learning; and although they discovered some interesting social rank differences, they too did not find any sex differences in individual learning (Latchem et al. 2025).

In conclusion, we found that *N. pulcher*, a group-living cichlid fish from Lake Tanganyika, could remember for 48 days. We also found that acute stress had a modest negative impact on learning but enhanced memory. In the wild, many animals could be chronically stressed due to hunger or environmental disturbances such as habitat fragmentation and climate change (Dickens and Romero 2013). Chronic stress differs in important ways from acute stress and likely impacts behaviour differently (Sørensen et al. 2013). Future work should examine the impacts of chronic stress on learning and memory. Finally, here we focused on a foraging task, but it would be worthwhile to also examine a spatial learning task such as a maze or another ecologically salient navigational cognitive capacity where cognitive sex differences are expected to be pronounced.

Acknowledgements We wish to thank Dr. Bruce Milliken for subject matter input on our study and we wish to thank Emma Esau, Gabriela Faragitakis, Easton Kusey, Andrew Millar, Tatum Taylor, and Yana Vaynberg for scoring over 1,600 videos. We wish to acknowledge the support of Natural Sciences and Engineering Research Council (NSERC) in the form of a Discovery grant to SB and the Ontario Graduate Scholarship Fund, and McMaster University for providing scholarship funds for EL.The authors thank the two anonymous referees and the associate editor, Tyrone Lucon-Xiccato, for their constructive comments which improved the paper.

Author contributions All authors contributed to the study conception and design. Conceptualization, material preparation, methodology, data collection, formal analysis, investigation, software, validation, and visualization were performed by C.C., with assistance from E.L. and S.B. All figures and tables were created by C.C and E.L. The first draft of the manuscript was written by C.C. All authors commented, reviewed, and edited previous versions of the manuscript. All authors approved the final manuscript.

Funding This study was funded by the Natural Sciences and Engineering Research Council of Canada Discovery Grant (#RGPIN2022-05353) awarded to Sigal Balshine, and an Ontario Graduate Scholarship awarded to Elias Latchem. The funders were not involved in any aspect of the study.

Data availability All data and R code (for figure creation and analysis) that were used in the manuscript can be found in the Zenodo repository, https://doi.org/10.5281/zenodo.17613952.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethics approval Collection, animal housing, and experimental procedures employed in our experiments were reviewed and approved by the McMaster University Animal Research Ethics Committee (AUP: 22-03-09). This study was in agreement with guidelines set forth by the Canadian Council on Animal Care (Olfert et al. 1993). During experimentation, our trials were regularly reviewed by the McMaster University Animal Care Committee. Upon completion of the experiments, fish were returned to their original social groups in their social tanks. Aggression was thoroughly monitored upon the return of the individuals, and no indication of distress or discomfort was observed.

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