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Influence of familiarity and sex on social learning in a group living fish

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ABSTRACT

Social learning, learning via observation and imitation, is an ability that can help animals adapt to their environment. Current research indicates that familiarity between the demonstrator and learner increases the likelihood that animals engage in social learning. Sex differences in philopatry can result in the more philopatric sex having a higher degree of familiarity with its groupmates than the dispersing sex. The aim of this study was to test how familiarity and sex affect social learning in the matrilineal, group-living cichlid species, *Neolamprologus pulcher*. A foraging assay was used to test the probability and speed of social learning in *N. pulcher*, and whether these were influenced by familiarity with the demonstrator, the demonstrator's sex, or the observer's sex. We found that familiarity did not have a clear effect on *N. pulcher* learning. Although demonstrator sex had no impact on learning, female *N. pulcher* learned faster than their male counterparts. As one of the first experimental studies to examine the factors influencing social learning in social cichlid fish, here we build upon the existing body of literature on fish learning and explore how information spreads in groups. Such knowledge can shed light on the behaviours, as well as the dynamics, and transmission of cultural traits in cichlids and other animals, contributing to the growing understanding of decision-making and the cognition underlying cooperation in other taxa.

1. Introduction

Learning can help individuals better adapt to their environments and increase their chances of survival and reproduction (Camacho-Alpízar and Guillette, 2023; Stanbrook et al., 2020; Shettleworth, 2001). However, learning can also be challenging as it requires cognitive skills, such as attention and memory (Manning and Dawkins al., 2012). Animals usually learn by sampling their environments, but such sampling can be energetically costly and dangerous (Dunlap et al., 2017). One way that individuals can reduce the cost of learning is by observing and copying the behaviours and choices of other animals, a phenomenon known as social learning (Brown Laland, 2003; Laland, 2004; Stanbrook et al., 2020). By observing what others do, individuals can learn skills (e.g., tool use) or obtain valuable information (e.g., such as where food might be or the reputation of a competitor). Social learning has been shown to occur across a wide variety of taxa, including invertebrates, mammals, birds, reptiles, and fishes (Camacho-Alpízar and Guillette, 2023; Laland et al., 2003) and can be used in variety of contexts, such as learning about new food sources (Choleris et al., 1998), determining what substrates to breed on (Sarin and Dukas, 2009), and selecting a mate (Dugatkin and Godin, 1997).

Social learning, observing others and then using this socially learned information, is a cheap but potentially unreliable way to learn. Social learning can reduce temporal and metabolic costs, as well as the inherent risks (e.g., encountering predators) associated with directly sampling the environment (Lee and Thornton, 2021; Munch et al., 2018). However, a major drawback of using socially learned information is that the observer is unable to fully verify the quality and veracity of the information, and so they must rely on incomplete data that may be suboptimal (Camacho-Alpízar and Guillette, 2023; Lee and Thornton, 2021). For example, guppies (*Poecilia reticulata*) have been shown to follow a socially learned path to access food, even when more direct routes were available (Laland and Williams, 1998). Similarly, domestic dogs (*Canis familiaris*) preferred a more conservative and socially learned behaviour to acquire a target, even though it was the more complex option (Pongrácz et al., 2003).

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As socially learned information can be unreliable, it would be maladaptive to exclusively rely on social information (Galef Laland, 2005). Instead, individuals must carefully choose the appropriate setting to employ social learning. The choice of when to use social learning can be influenced by many factors such as the difficulty of the task, the complexity of the environment, or the internal state of the learner (Camacho-Alpízar and Guillette, 2023; Munch et al., 2018). Animals might also base their choice about when to use social learning based on *who* they are learning from. Social learning theory suggests that increased familiarity between the demonstrator and observer improves the chances that social information will be used (Camacho-Alpízar and Guillette, 2023). Familiar individuals, like parents or relatives, often have more relevant experiences, and therefore can provide more beneficial and reliable information for learners (Camacho-Alpízar and Guillette, 2023). Furthermore, a familiar individual has the ability to reduce stress for a learner, which can improve an individual's capacity to learn (Figueroa et al., 2013). Hence, learning from familiar individuals may be a more effective and efficient way to learn. In fact, familiarity has been shown to have a positive effect on learning in species, such as the White's skink (*Liopholis whitii*), where observers learning from familiar demonstrators learned more readily and made fewer errors than observers that learned from unfamiliar demonstrators (Munch et al., 2018). Likewise, domestic pigs (*Sus domesticus*) accepted a novel food only if they learned about the diet items from a familiar demonstrator, and would not accept novel food that they witnessed an unfamiliar pig eating (Figueroa et al., 2013). However, this preference for familiarity has not been observed across *all* animals.

There are a handful of species where research has shown the opposite, that individuals learn best from unfamiliar demonstrators. This phenomenon has been named the 'novel social partner' hypothesis (Ramakers et al., 2016), and it has been observed in Peter's tent-making bats (*Uroderma bilobatum*), with individuals copying food choices from unfamiliar demonstrators rather than from their familiar groupmates (Ramakers et al., 2016). Norway rats (*Rattus norvegicus*) also have a slight preference for learning food cues from unfamiliar individuals (Galef and Whiskin, 2008). So why would such a preference to learn from unfamiliar individuals evolve? Perhaps the preference for, or interest in, unfamiliar or novel things (neophilia) means that animals pay more attention to unknown conspecifics and do so because these novel things or individuals could pose a threat or be a potential mate (Lucon-Xiccato et al., 2019; Valvo et al., 2019). Giving increased attention to particular individuals could impact and lead to better learning (Castro and Wasserman, 2014; Nityananda, 2016). Copying unfamiliar demonstrators can also be a way for new information to enter a social group and can circumvent information bottlenecks (Ramakers et al., 2016). Galef and Whiskin (2008) found that focal rats sniffed unfamiliar rats for longer than familiar ones. They theorized that the prolonged sniffing of an unfamiliar rat compared to a familiar rat could lead to greater information sharing, specifically about food, and thus impact food selection to match the unfamiliar rather than the familiar conspecifics preferences and food choices. In general, increased attentiveness and observation for the unknown may influence learning. Yet, these examples also demonstrate that the role familiarity plays in social learning is dynamic and species and context dependent.

Sex can also influence social learning (Camacho-Alpízar and Guillette, 2023). The 'copy the philopatric sex' hypothesis proposes that there should be a preference to copy the sex that does not disperse or simply stays closer to its natal territory and relatives. The philopatric sex has more opportunities to form closer ties with other non-dispersing individuals, and therefore individuals of this sex are more likely to have and provide more relevant, environment-specific information (Camacho-Alpízar and Guillette, 2023). For example, vervet monkeys (*Chlorocebus pygerythrus*) preferentially learn from females who remain with their natal groups, compared to males who eventually disperse (van de Waal et al., 2010). In African striped mice (*Rhabdomys pumilio*), juveniles relied on information received from their philopatric mothers more than their roving fathers (Rymer et al., 2008).

The sex of the observer could also impact social learning. In many species females are less bold and less exploratory than males (Brown et al., 2007; King et al., 2013; Schürch and Heg, 2010), which could lead to females having fewer opportunities to sample their environment, and thus increase their dependence on social learning (Choleris and Kavaliers, 1999). Female chimpanzees (*Pan troglodyte*) were 15–24 % more likely to use social information to solve experimental tasks than males (Watson et al., 2018). In Atlantic mollies (*Poecilia mexicana*), both the males and females managed to socially learn to pick up a coloured disc, however males chose more accurately but females selected the disc faster (Fuss et al., 2021). Therefore, differences in activity and exploration between males and females may influence the likelihood of engaging in social learning and may determine when social learning is employed.

To better understand how familiarity and sex influence social learning, we examined learning in the group-living cichlid, *Neolamprogus pulcher*. This small African fish, endemic to Lake Tanganyika, is a well-studied model species for group living and cooperation. It is a highly social species that lives in stable hierarchical groups with two dominant breeding individuals and typically five to nine subordinate helper fish of both sexes that help the dominant pair breed (Taborsky, 2016; Wong and Balshine, 2011). Each social group lives on a territory in close proximity to other groups within colonies (Stiver et al., 2004). These spatial arrangements provide individuals regular opportunities to learn from both familiar groupmates and neighbours (Balshine et al., 2001; Stiver et al., 2005; Taborsky, 2016; Wong and Balshine, 2011). Previous studies demonstrate that this fish species is capable of rapid and accurate discrimination between familiar and unfamiliar individuals (Kohda et al., 2015; Salena, 2020), and that familiarity reduces aggression, which may promote learning (Frostman and Sherman, 2004; Hick et al., 2014; Jordan et al., 2009; Salena, 2020). Cichlids in general have been shown to have developed cognitive abilities, such as memory of past social interactions (Félix and Oliveira, 2021; Jordan et al., 2021; Salena and Balshine, 2020) and one cichlid species, *Julidochromis transcriptus*, was able to remember conspecifics up to five days (Hotta et al., 2014), indicating that they likely remember specific individuals over time. Finally, *N. pulcher* is a matrilineal species, so females are philopatric and provide more parental care than the males (Desjardins et al., 2008; Dierkes et al., 2005; Wong et al., 2012). Thus, female fish may have more opportunities to learn from their social group and demonstrate their knowledge compared to their male counterparts. There is currently limited research on the specific contexts *N. pulche*r use social learning, however, Taborsky et al., (2012) showed that when reared with older fish, individuals learned to behave in a more socially appropriate manner. Moreover, in the field, other species of fish have been shown to socially learn about shelter, predator avoidance, and foraging (Brown Laland, 2003; Laland et al., 2003, 2011) and it is likely that group living *N. pulcher* will use social information to learn about such factors as well.

We tested how familiarity, demonstrator sex, and observer sex affect social learning by examining whether *N. pulcher* observers learn a novel foraging task more frequently or more quickly based on familiarity with the demonstrator, sex of the demonstrator, and sex of the observer. This particular foraging task has been previously employed before to study individual and social learning in *Neolamprologus pulcher* (Culbert et al., 2020, 2021; Guadagno and Triki, 2024; Latchem et al., 2025; Stanbrook et al., 2020) and in other fish species (Buechel et al., 2018: Fuss et al., 2021; Lucon-Xiccato and Bisazza 2014). We predicted that *N. pulcher* observers would learn more frequently and faster from familiar demonstrators because this cichlid fish species is highly social and often lives its entire life with the same group of familiar fish (Wong and Balshine, 2011). Group members share a territory and thus will likely have more relevant, reliable, and beneficial environmental information compared to unfamiliar individuals from other social groups and colonies (Camacho-Alpízar and Guillette, 2023; Hick et al., 2014; Jordan et al., 2009; Thünken et al., 2016). Also because female *N. pulcher* remain in or near their natal territories (Stiver et al., 2007), females are more likely to have pertinent environmental information. Therefore, we also predicted that observers with female demonstrators and female observers would learn more readily.

2. Methods

2.1. *Study animals*

We conducted our social learning experiment in the Aquatic Behavioural Ecology Laboratory at McMaster University, Hamilton, Ontario, Canada from June to September 2023 using the African cichlid, *Neolamprologus pulcher*. The fish used were laboratory-reared descendants of wild-caught fish from the southern shores of Lake Tanganyika in Africa.

2.2. *Housing*

Prior to the experiment, we housed all experimental fish in their original social groups (1 dominant female, 1 dominant male, and approximately 5–7 helper fish) in 190-L glass tanks (91 cm×41 cm x 51 cm). Fish had lived in their social groups for 6 months prior to the start of the experiment. Each social group tank contained a heater, mechanical filter, air stones, two half-clay pots, and two mirrors. The tanks were lined with a crushed coral sand substrate. The water temperature was maintained between 24.0°C - 27.0°C. The fish were fed commercially available fish flakes (Nutrafin A7134 Basix Cichlid Food) until satiation six times a week and were held under a 12:12-hour light: dark cycle with 30 min of fade on/off to mimic dawn and dusk.

2.3. *Experimental tank set-up*

The methods for the social learning experiment set up were adapted to fit the requirements our study from the methodology outlined by Buechel et al., (2018); Fischer et al., (2021); La Loggia et al., (2022) and first developed by Lucon-Xiccato and Bissaza (2014) for guppies. Such learning paradigms based on lifting discs for food rewards were first employed and tested in *N. pulcher* by Culbert et al. (2020) and Stanbrook et al. (2020); and then further tested by Guadagno and Triki (2024); and Latchem et al. (2025). Our social learning experiment was run in twelve long 75 L learning tanks (each measuring 75 cm×32 cm x 32 cm). These learning tanks were divided into three compartments: two equally sized compartments on each end of the tank (30 cm x 32 cm x 32 cm) and one smaller middle compartment (15 cm x 32 cm x 32 cm). Each social learning tank was fitted with an air stone, a heater, and a mechanical filter. A crushed coral sand substrate covered the floor of each tank. The back and sides of the tanks were covered with opaque blue adhesive paper to prevent glare and the fish from seeing other learning tanks. Conversely, the front of the tank was left clear to permit video recordings of the trials. The three compartments were separated by movable clear and black opaque plastic partitions. The centre compartment held a white plastic feeding tray (10 cm x 5 cm x 2 cm) with ten face-up wells (depth of well: 9 mm), whereas each outer compartment contained a half clay pot that the fish used as shelter (Fig. 1a).

2.4. *Fish used for the Social Learning Experiment*

In the social learning experiment, we had 47 unique observers and 32 demonstrators. Sixteen of the demonstrators lifted the disc as trained for

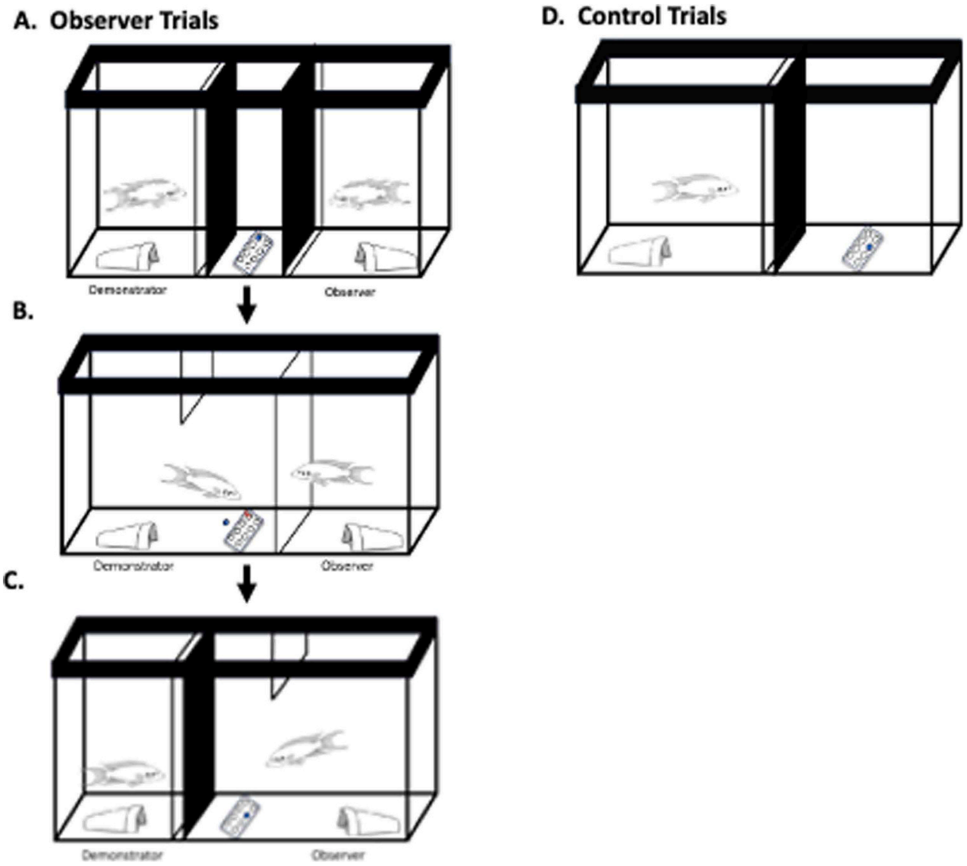

Fig. 1. (a) The social learning trials experimental tank setup. (b) A demonstration trial depicting the demonstrator fish moving the plastic disc off the feeding tray while the observer watches from behind the clear barrier. (c) An observer trial showing the observer fish making a choice by the feeding tray during which the demonstrator is hidden behind the black opaque barrier. (d) Control trials experimental tank set up (side view).

only one observer, while another 16 fish did the same demonstration but for two different observers. Each demonstrator was housed with only one observer at a time, and demonstrators that had two observers were not re-used until they had cycled through the entire experiment with their first observer. Demonstrator fish had all been previously trained to move a coloured disc off a feeding tray to obtain a 5 mm blood worm food reward that had been placed underneath the disc, whereas observers were completely naïve to this task and had never seen or interacted with the feeding trays and discs. Half of the demonstrators had learned to move a yellow disc, while the other half had learned to move a blue disc to get food rewards. A single demonstrator was placed into one of the outer compartments of each learning tank and was given 24 h to acclimate to the tank. To check that all trained demonstrators were moving the discs consistently, we raised the black and clear barriers near the demonstrator, so that the demonstrator could enter the centre compartment where they could interact with the tray. Demonstrators were given five minutes to move the disc; the disc was always the same colour as the one they had been trained on. Typically, once the demonstrator had moved the disc and eaten their reward, they would return to their end compartment on their own. However, when necessary, we gently guided the demonstrator back to their comparement with the barriers. After the barriers were replaced, we would reset the food tray. We repeated this feeding task (placing and covering the blood worm in a new random well each time) to make sure demonstrators were consistently moving the disc. Once the demonstrator had moved the disc three consecutive times, they were considered trained and were immediately started in the social learning experiment. If the demonstrator did not move the disc consistently, we retrained them (see Latchem et al., 2025); retraining took 1–3 days. We had to replace three demonstrators because despite originally learning the task, these three fish did not consistently move the disc in the social learning tanks even after three days of retraining.

Once all 32 demonstrators were consistently moving the plastic disc, we placed a naive observer fish in the other opposite outer tank compartment of each social learning tank (Fig. 1a). Note the end chamber sides in which demonstrators vs observers were placed were randomized for each learning tank by flipping a coin. Demonstrators and observers were paired so that they were either familiar with one another (which was defined as both fish coming from the same social group and having lived together in the same social housing tank for six months prior to the experiment, N = 24) or were unfamiliar (which was defined as the demonstrator and observer not being from the same social group, N = 23). We used both male and female demonstrators and observers, with 8 tanks containing female-female pairs, 17 pairs containing male-male pairs, and 22 pairs being mixed sex pairs. Due to having a limited number of demonstrators, we could not size and sex match our observer and demonstrator pairs. On average, demonstrators were 2.51 mm smaller (median: 0.50 mm; range: −53.9 mm – 57.72 mm) and 0.19 g lighter than observers (median: 0.34 g; range: −19.32 g – 16.43 g). See Supplementary Materials for more information about demonstrator and observer pairings. Each observer was given 24 h to acclimate to its own compartment of the social learning tank with all the barriers down and then they were given one hour to explore the centre compartment and interact with the empty feeding tray. During this one hour period, the demonstrator was hidden behind both a black and transparent barrier, and there was no plastic disc nor food reward in any of the wells. After the hour, we gently guided the observer back to its compartment with the barrier and the learning trials began.

2.5. Social learning experiment procedures

Before each trial, we placed a 5 mm blood worm into a random well on the feeding tray and fully covered it with a plastic disc. The colour of the disc always matched the colour learned by that particular demonstrator. The black barriers were in place while we positioned food into the wells to obstruct both the demonstrator's and observer's view into the centre compartment. After the disc was placed over the well (i.e. the food was hidden), we removed the opaque barriers allowing both fish to see each other and the feeding tray.

To start a demonstration trial, we raised the clear barrier on the demonstrator's side and gave the demonstrator two minutes to move the disc off the tray while the observer watched from behind its clear barrier (Fig. 1b). Once two minutes passed, we gently guided the demonstrator back into its compartment with a barrier, lowered the clear barrier, and replaced both black barriers. We then reset the feeding tray and started the subsequent trial after about five minutes. We repeated this process for a total of five demonstration trials. So, each observer fish saw the demonstrator lifting a disc and eating the food reward underneath five times before it was given a chance to move a disc and get a food reward itself.

After five demonstration trials were complete, we ran one observer trial. Similar to the demonstration trials, before the start of an observer trial, we placed a 5 mm blood worm into a random well on the feeding tray and fully covered it with a disc. During the observer trials, we lifted both of the observer's barriers allowing the observer to access the middle compartment (Fig. 1c). However, we did not lift either of the demonstrator's barriers during the observer trials, so the demonstrator was blocked from view which prevented any interactions between the two fish and allowed the observer to focus their attention on the food tray. The observer was given five minutes to move the disc, after which we would gently guide them back to their compartment. We ran five demonstration trials and one observer trial twice a day with an approximate one-hour break between sets, with a total of ten demonstration trials and two observer trials run per day. Trials ran until the observer "learned" (i.e., used their head or mouth to move the disc in three consecutive trials) or when 12 days of experiments had elapsed (i.e., a maximum of 24 observer trials). Although, the learning criterion (i.e., moving the disc in three consecutive trials) is lower than in some other experiments, we selected this threshold to prevent observers from learning the task independently.

If a demonstrator fish did not move the disc on a particular trial, we would immediately repeat the trial. If the demonstrator fish again failed to move the disc on the repeated trail, we ended that set of trials. If the failure happened in the first set of five trials, we would proceed to the second set of five trials after a one-hour break, starting from the first trial attempt. If the failure happened in the second set of five trials, we would end trials for the day and continue the subsequent day, starting from the first trial of the first set. Demonstrators and observers were always fed flakes until satiation at the end of each experimentation day in their own end chamber.

2.6. Control trials

To ensure that the social learning was in fact social learning and not individual learning, we also ran 18 control trials where fish did not see a demonstration of the task. We asked if naïve fish could learn to move the disc independently (i.e., without observing a demonstrator fish). The 18 control fish used were naïve and had never seen or interacted with the feeding trays or plastic discs before these control trials.

The control trials took place in six 40-L tanks (50 cm×26 cm x 30 cm) each fitted with an air stone, heater, and a mechanical filter. The back and sides of the tanks were covered with opaque blue adhesive paper, while the front was left clear to record the trials. A crushed coral sand substrate covered the tank floor. The control tank was divided into a front and back compartment of equal size (25 cm×26 cm x 30 cm); the front compartment contained the same white plastic feeding tray used in the demonstration trials (see above), while the back compartment contained a half clay pot that was used as shelter. The two compartments were separated by a single black plastic removable partition. We placed the naïve control fish in the back compartment of each control tank and gave them 24 h to acclimate (Fig. 1d). Following this acclimation period, we lifted the black barrier, and each control fish was given one hour to explore the front compartment with the empty, uncovered feeding tray. After the hour, we guided the fish back to their compartment and began the control trials.

To start the control trials, we placed a 5 mm bloodworm in a randomly selected well and fully covered the well with a plastic disc. Then, we raised the black barrier and gave the control fish five minutes to interact with the tray and move the disc. The feeding trays and discs used were identical to those used in the social learning experiment described above. After the five minutes elapsed, we gently guided the control fish into the back compartment. We repeated the control trials twice daily, with an approximate one-hour break between sets. Trials ran until the control fish had learned (i.e., used their head or mouth to move the disc in three consecutive trials) or when 12 days elapsed (i.e., a maximum of 24 control trials had been conducted), which ever occurred first.

2.7. *Familiarity experiment*

To determine whether the learner's personal preference for familiar or unfamiliar influenced the results, we also ran a separate familiarity trial for all 47 of the observer fish used in the social learning experiments. In these familiarity trials we investigated whether the observer fish, which we called the 'focal fish' in this experiment, spent more time near a familiar or unfamiliar fish.

The familiarity trials took place in a 189 L tank (96 cm×46 cm x 43 cm). The back and sides of the tanks were covered with opaque blue adhesive paper, while the front was left clear to record the trials. The tank was divided into three equal compartments (32 cm×46 cm x 43 cm). The middle compartment was separated from both side compartments by a clear plastic partition and a black plastic removable partition. The middle compartment contained a clear cylindrical tube (10 cm diameter). Black markings on the floor of the middle compartment divided the space into four equal quadrants lengthwise, each 8 cm wide.

Before starting the familiarity experiment, we placed one fish into each side compartments; these fish were size and sex matched to each other. One side of the tank we placed a fish familiar to the focal fish while on the other side of the tank we placed an unfamiliar fish. Just as in the social learning experiment, familiar fish were from the same original social group (i.e., they lived together for six months) and the unfamiliar fish were from different social groups (i.e., they had not lived together before). Neither the familiar nor unfamiliar stimuli fish used in this familiarity experiment were used as demonstrators in the social learning experiment. The focal fish were always held in the cylindrical tube for five minutes to acclimatize to the tank before the trial started. During this period both the familiar and unfamiliar stimuli fish were not visible to the focal because there were black plastic barriers preventing the fish from seeing the end chambers.

To begin the trial, we simultaneously raised the cylindrical tube and both black plastic barriers, this allowed the focal fish to see both fish in the end compartment and move around the middle compartment. We recorded the focal fish's location relative to the black grid markings on the floor and quantified how much time each focal fish spent near either the familiar or unfamiliar fish. After the 10 min elapsed, we ended the trials, removed the fish, mixed the water, and reset the tank for the next trial with a new focal (observer) and two new stimuli fish.

2.8. *Video recordings and scoring*

Both the social learning experiment and the familiarity experiment trials were recorded from the front of the tanks on Sony 4 K cameras recording at 30 FPS. All videos were deidentified and scored in the Behavioural Observation Research Interactive Software (BORIS, version 8.25; Friard and Gamba, 2016) by observers who were blind to the identity of the fish. Three independent assistants helped score all the videos from September to December 2023 and their scores were checked for consistency and repeatability (overall ICC score of 0.93 across observers).

2.9. *Statistical analyses*

Statistical analyses of the data were performed using R (Version 2023.12.1 +402; R Core Team, 2023). Data were tested for normality, square root-transformed when necessary to achieve normality, and analysed with either parametric or non-parametric tests. A significance level (α) of 0.05 was used for all tests and the results of two-tailed tests are reported.

A chi-squared test was conducted to test the effects of familiarity, demonstrator sex, and observer sex on the percentage of observers that learned. We considered the fish to have learned once they moved the disc consistently across three trials (i.e., used their head or mouth to move the disc in three consecutive trials). We also ran a Fisher Exact Test to test whether the proportion of fish that learned without demonstrator (N = 18 control fish) differed from the proportion of fish that learned with demonstrators (N = 47 observers). We also used a Fisher Exact Test to explore if the number of control fish that learned varied from chance.

The differences in the number of trials to reach learning criterion between fish with familiar and fish with unfamiliar demonstrators was analyzed with Cox Proportional Hazard regression models (Survival package in R). A Cox proportional survival model is a semi parametric model, meaning it does not make any assumptions about the distribution of the data. Fish that failed to reach the learning criterion were coded as a 0 for the event variable in the model, while fish that successfully learned were coded as a 1. The number of trials that it took to reach the learning criterion was used for the time variable in the model. The assumption of proportional hazards was tested via a visual inspection of the Schoenfeld residuals against the transformed number of trials that it took the fish to learn. A DFBETA residual plot was used to check for influential observations (any residual greater than 1). We built three separate Cox models to examine the influence of familiarity, demonstrator sex and observer sex on learning speed. Finally, we built a model to test for interactions between familiarity, for demonstrator sex, and for observer sex (see Supplementary Materials).

In addition, unpaired *t*-tests were performed to test the effects familiarity, demonstrator sex, and observer sex had on the time the observers took to move the disc during the learning trials. Note, initially we had 24 familiar and 24 unfamiliar demonstrators; however, one demonstrator that had to be retrained to move the disc stopped moving the disc consistently late in the experiment. As this demonstrator stopped their demonstration behaviour late in the trial sequence, we could not replace it. Thus, we were able to complete trials only with 23 observer fish paired with unfamiliar demonstrators. Additionally, the camera malfunctioned in 31 of the 1328 recorded trials (0.02 % of trials recorded), so we could not calculate the average time it took for one of the fish to move the disc.

To analyze the data from the Familiarity Experiment, we ran a Wilcoxon signed-rank test to determine if focal fish preferred to spend more time near a familiar fish or near an unfamiliar fish. We compared the time fish spent in the half of the tank near the familiar fish with the time spent in the half of the tank near the unfamiliar fish. We then ran a Spearman rank correlation to measure the association between the time the focal fish spent near either the familiar or unfamiliar fish and their speed of learning (i.e., number of trials to reach the learning criterion).

3. Results

3.1. *Impact of familiarity on social learning*

Of the 47 observers, only 24 or 51 % managed to learn the task (i.e., they moved the disc off the feeding tray in three consecutive trials). Of the successful learners, 14 or 58 % were paired with a familiar demonstrator, and 10 or 42 % were paired with an unfamiliar demonstrator. Thus, there was no clear effect of familiarity of the demonstrators on the probability of social learning (Cramer's V = 0.11, Chi-squared test, $\chi^2 = 0.53$, df = 1, p-value = 0.47, Fig. 2a). On average, observers with familiar demonstrators took 14 trials (± 2 SE) trials to learn to move a disc while observers with unfamiliar demonstrators took a mean of 17 trials (± 2 SE). Familiarity was not a significant predictor for the number of trials taken to learn (Cox proportional hazards regression HR = 0.60, 95 % CI [0.26, 1.34], z = -1.26, p-value = 0.21, Fig. 2a), providing further evidence that familiarity does not appear to play a role on whether the fish learned socially. When we compared the time it took observers to move the disc in each trial, observers learning from familiar demonstrators took a mean of 96 s (± 16 SE) to move the disc off the feeding tray while observers learning from unfamiliar demonstrators took on average 72 s (± 13 SE). Again, this difference was not significant (Cohen's d = 0.46, unpaired *t*-test, t = 1.09, 95 % CI [-21.82, 69.93], df = 21, p-value = 0.29, Fig. 2b).

3.2. Impact of demonstrator sex on social learning

Of the 24 observers that did learn, 10 or 42 % had a female demonstrator and 14 or 63 % had a male demonstrator. Demonstrator sex did not significantly impact learning outcomes (Cramer's V = 0.02, Chi-squared test, $\chi^2 = 0.01$, df = 1, p-value = 0.90, Fig. 2c). Observers with female and male demonstrators both took on average 15 trials (± 2 SE) to reach the learning criterion. Demonstrator sex did not appear to have a significant impact on the number of trials needed to learn (Cox proportional hazards regression HR = 1.25, 95 % CI [0.55, 2.86], z = 0.53, p-value = 0.59, Fig. 2c). Further, observers with a female demonstrator took on average 72 s (± 11 SE) to move the disc, whilst observers with a male demonstrator took slightly longer with a mean of 98 s (± 18 SE). However, this difference in the average time it took to move the disc in relation to demonstrator sex was not significant (Cohen's d = 0.37, unpaired *t*-test, t = -1.22, 95 % CI [-71.74–18.71] df = 21, p-value = 0.24, Fig. 2d).

3.3. Impact of observer sex on social learning

Of the 47 observers tested (27 males and 20 females), 44 % of males learned (N = 12) and 60 % of females learned (N = 12). Thus, the percentage of males versus females that learned did not differ (Cramer's V= 0.07, Chi-squared test, $\chi^2 = 0.58$, df = 1, p-value = 0.45, Fig. 2e). However, female observers took fewer trials to learn, needing an average of 12 (± 1 SE) trials to learn from demonstrators on how to get food rewards compared to about 17 trials (± 2 SE) needed by males (Cox proportional hazards regression model HR = 0.36, 95 % CI [0.26, 1.34], z = -2.17, p-value = 0.03, Fig. 2e). Moreover, female observers took much less time to move the disc per trial, with a mean of 60 s (± 9 SE), whilst male observers took nearly twice as long with a mean of 113 s (± 17 SE) (Cohen's d = 0.93, unpaired *t*-test, t = -2.70, 95 % CI [-92.62–11.95], df = 21, p-value = 0.01, Fig. 2f).

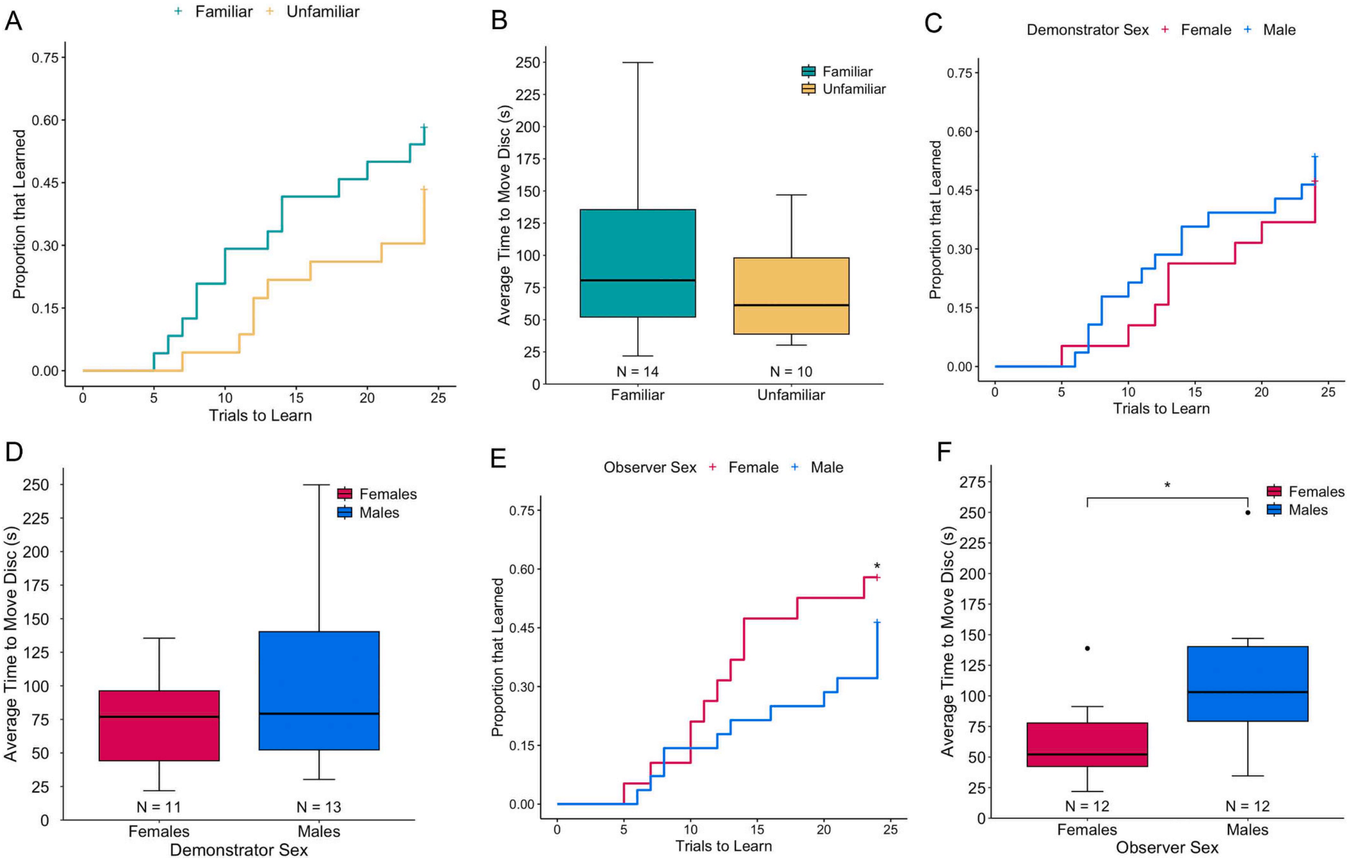

Fig. 2. (a) Proportion of fish that learned and number of trials it took to learn based on whether the fish were familiar with their demonstrator (b) the average time (in seconds) it took observer fish that learned to move the plastic disc off the feeding traying according to whether they were familiar (turquoise) or unfamiliar (yellow) with their demonstrator. (c) Proportion of male versus female observer fish that learned and number of trials it took to them learn based on the sex of their demonstrator. Blue shows the trials where the demonstrators were male, and the red shows the trials where the demonstrators were female (d) The average time (in seconds) it took observer fish that learned to move the plastic disc off the feeding traying according to their demonstrator's sex. Blue shows the trials for observers when the demonstrators were male and red shows the trials where the demonstrators were female (e) Proportion of male versus female observer fish that socially learned and the average time it took them to learn based on their own sex. Blue represents male observers and red represents female observers (f) The average time (in seconds) it took observer fish that learned to move the plastic disc off the feeding traying based on whether they were male (blue) or female (red). Boxes depict medians, first and third quartiles, and 1.5 × the upper and lower interquartile ranges; points represent individual values.

3.4. Control trials

Of the 18 control fish without demonstrators, none learned the task (i.e., no fish moved the disc in three consecutive trials). This failure to learn differed significantly from random chance (Fisher's Exact Test, $p = 0.001$). When we compared the proportion of control fish that learned without demonstrators (0/18 learned) with the proportion of fish that learned and were paired with demonstrators (24/47 fish learned), the fish in the Social Learning Experiment (that had demonstrators) were much more likely to learn (Fisher's Exact Test, $p < 0.0001$).

3.5. Influence of familiarity trials on social learning

Our focal fish did not show a clear preference for either familiar or unfamiliar fish in the Familiarity Experiment (Matched-pairs rank-biserial correlation $r_{pb} = 0.04$, Wilcoxon signed rank, $W = 428.5$, $N = 47$, $p = 0.78$). Moreover, there was no correlation between the time spent near familiar fish and the time it took to learn (Spearman ranked correlation, $Rho = 0.02$, $N = 47$, $p = 0.90$). Similarly, there was no correlation between time spent near familiar fish and time to move the disc ($Rho = 0.04$, $p = 0.85$).

4. Discussion

Animals that live in social groups have more opportunities to engage in social learning than solitary species and regularly gain and share information with individuals around them. Familiarity and sex are thought to influence an animal's decision to engage in social learning (Camacho-Alpízar and Guillette, 2023; Figueroa et al., 2013; Munch et al., 2018; Thünken et al., 2016). In this study, we built on the existing literature by investigating if and how familiarity and sex influence the speed and likelihood of social learning in the group living cichlid fish, *N. pulcher*. In general, familiarity did not impact social learning, nor did the sex of individual doing the demonstration. However, female observers learned from others more quickly and moved a disc to get food rewards faster than males.

4.1. Observer sex

As we predicted, female observers learned faster than male observers. This difference in social learning may be due to the difference in female and male dispersal patterns in *N. pulcher*. Females are less likely to disperse from their natal territories (Desjardins et al., 2008; Dierkes et al., 2005; Stiver et al., 2006; Wong et al., 2012). Moreover, female *N. pulcher* tend to be less exploratory than males (Schürch and Heg, 2010), which may result in fewer asocial learning opportunities. This lack of individual learning opportunities might make female *N. pulcher* more willing to use social learning. Females stay in their natal territories, so they may benefit more from copying other group members than their male counterparts who will eventually leave for other territories where the behaviours they had learned socially may no longer be relevant. A similar pattern has been found in vervet monkeys (van de Waal et al., 2010) and ninespine sticklebacks (*Pungitius pungitius*), where females relied more on social information and males generally relied on asocial learning (Webster Laland, 2010). It should be noted that this difference in learning preference in sticklebacks was found in only gravid females, and the males generally relied on asocial learning, increasing their ability to forage and establish or defend territories.

4.2. Familiarity

We predicted that individuals would find it easier to learn from familiar demonstrators as has been observed in a wide variety of species (Figueroa et al., 2013; Munch et al., 2018). However, we found no difference in learning outcomes between familiar and unfamiliar *N. pulcher* demonstrators. Familiar individuals were expected to be preferred demonstrators as familiarity reduces aggression, which promotes learning (Jordan et al., 2009), and previous studies in cichlids have shown that the cichlids have social memory which would allow them to recognize familiar individuals and adjust their behavior accordingly (Kohda et al., 2015; Félix and Oliveira, 2021; Salena, 2020; Salena and Balshine, 2020). Moreover, familiar individuals typically would have more relevant, and therefore more useful, information (Camacho-Alpízar and Guillette, 2023). Given that *N. pulcher* typically maintain stable social groups over extended periods of time (Balshine et al., 2001), unfamiliar fish may possess different experiences or information that could be valuable to observers. As mentioned above, unfamiliar individuals can bring in novel information, which can help avoid information bottlenecks for group living animals (Ramakers et al., 2016). In our experiment, one challenge may have been that the observers with unfamiliar demonstrators would have generally become somewhat more familiar with them across the learning trials (up to 120 trials). That said, the unfamiliar observer and demonstrator pairs of fish were never allowed to directly interact, had a maximum of 20 min a day to interact across a barrier, and so were never able to perform normal social behaviours. In contrast the familiar pairs knew each other extremely well, having previously lived together for six months where they interacted daily. Thus, there was still a considerable difference in the degree of familiarity between the unfamiliar and familiar pairs due to the prior experiences. To provide an experience of truly unfamiliar demonstrator, would have required the use new unknown demonstrators for each trial (up to 120). Logistical challenges of training that many demonstrators as well as the stress caused by moving fish in and out of social learning tanks prevented us from adopting this design. Additionally, due to space and tank constraints in the lab, control fish were tested in a slightly different tank setup compared to non-control (social learning) fish. Although, the tank environment was standardized, slight differences in tank configuration may have contributed to minor variation in behaviour between control and non-control fish.

Another potential explanation why our observers did not learn faster from the familiar demonstrator is that whereas the observer and demonstrator were familiar with each other, they were not necessarily kin. In the wild, natural selection may favour learning between kin, not merely those who are familiar with one another, because there is more benefit in sharing knowledge between related individuals due to kin selection (Figueroa et al., 2013). This distinction between familiarity and kinship is particularly relevant to *N. pulcher* because although the social groups contain many relatives, non-related conspecifics can and do join a social group (Le Vin et al., 2010; Stiver et al., 2005). In our study, it was difficult to determine whether kinship played a role as we did not genotype the fish and did not have access to the genealogical relationships. Both visual and olfactory cues are required to determine kin in *N. pulcher* (Le Vin et al., 2010), and the olfactory cues may have been limited due to lack of physical contact between the demonstrator and observer. Our study did not reveal a clear preference for familiar fish. Thus, although kinship effects cannot be ruled out entirely, our experimental design did not provide a way to directly measure its impact. Future research should try to tease apart how kinship and familiarity may interact to influence social learning, ideally under conditions where both visual and olfactory cues are readily available.

4.3. Demonstrator sex

We predicted that observers would prefer female demonstrators over male demonstrators because females are the more philopatric sex (Dierkes et al., 2005) and will therefore know the territory and its resources best (Wong et al., 2012). Additionally, female *N. pulcher* breeders are often more closely related to the helpers than the breeding males (Dierkes et al., 2005; Stiver et al., 2005; Hellmann et al., 2015). However counter to our expectations, we did not have any clear evidence to support the idea that observers preferentially learn from female demonstrators. One potential reason why the philopatric sex might not have been better demonstrators is that because males are typically more exploratory and are more likely to leave their natal groups (Brown et al., 2007, Desjardins et al., 2008; Dierkes et al., 2005; King et al., 2013), which means they have more opportunities to for asocial learning. So, although females may be more knowledgeable about their territories, males may be bringing in new information and novel behaviours to the group making them useful demonstrators. Therefore, observing both male and female demonstrators may have benefits in *N. pulcher* groups such as preventing information bottlenecks, but this theory requires more research.

4.4. A note about the social learning assay

We used this particular learning assay for food because it had been well tested in *N. pulcher* and other fish species and food provides a reliable and repeatable motivator for learning (Buechel et al., 2018; Culbert et al., 2020, 2021; Fuss et al., 2021; Latchem et al., 2025; Lucon-Xiccato and Bisazza, 2014; Stanbrook et al., 2020). In the wild, *N. pulcher* regularly moves snails, sand and debris from their territories and shelters, and do so with their mouths (Heg and Taborsky, 2010) so moving discs out of the way to get a food reward seemed like a behaviour that they could readily learn. We also surmised that *N. pulcher* do regularly use social learning in a foraging context. Although in the wild *N. pulcher* mainly feed on zooplankton acquired in the water column and feed there with other conspecifics (Balshine et al., 2001, Wong and Balshine, 2011), for the first 6–12 months of life these fish mostly feed on zooplankton gleaned from the substrate and in their territories (S. Balshine pers obs). Even large adult *N. pulcher* will occasionally eat organisms off the substrate, especially in the early morning and late evening in their sub-territories and shelters or whenever there are few zooplankton in the water column (S. Balshine per obs). So, it is likely that *N. pulcher* can and do learn socially about **what** to eat when foraging on the ground and that such learning may be highly relevant for young fish. We also expect that *N. pulcher* regularly socially learn about **when** it is safe or efficient to feed and where it is safe or efficient to feed (i.e., how high to go in the water column). However, we expect that *N. pulcher* may also be socially learning about safety (which individuals and species are dangerous), about their territory and shelter quality (where there are good places to hide). It is possible that familiarity plays a role in the likelihood of individuals acquiring socially relevant information in other more natural contexts, such as learning about shelter availability and safety (Stanbrook et al., 2020) or how to appropriately display and signal (Taborsky et al., 2012). Experiments addressing these other important social learning domains would be highly interesting.

5. Conclusions

Although familiarity and the sex of the demonstrator did not affect social learning in *N. pulcher,* female observers learned faster than males. Future studies should explore the mechanisms that underly these sex differences. Ultimately, determining the characteristics that impact social learning in animals will provide insights into how individuals learn from one another and how information spreads in groups. Such knowledge can increase our general understanding of social behaviour, cultural transmission, and cooperation versus competition in group-living fish and other taxa.

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), in accordance with guidelines set forth by the Canadian Council on Animal Care (Olfert et al., 1993). Our practices are subject to regular review by the McMaster University Animal Care Committee during experimentation.

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CRediT authorship contribution statement

Elias Latchem: Writing – review & editing, Visualization, Validation, Software, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **Grace Ogundeji:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Sigal Balshine:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare no conflict of interest.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2025.105307.

Data Availability Statement

All manuscript data and R code for analysis and figure generation was archived on Zenodo https://doi.org/10.5281/zenodo.15538824.

References

Balshine, S., Leach, B., Neat, F., et al., 2001. Correlates of group size in a cooperatively breeding cichlid fish (Neolamprologus pulcher). Behav. Ecol. Socio 50, 134–140. https://doi.org/10.1007/s002650100343.

Brown, C., Laland, K.N., 2003. Social learning in fishes: a review. Fish Fish 4, 280–288. https://doi.org/10.1046/j.1467-2979.2003.00122.x.

Brown, C., Jones, F., Braithwaite, V.A., 2007. Correlation between boldness and body mass in natural populations of the poeciliid *Brachyrhaphis episcopi*. J. Fish. Biol. 71, 1590–1601. https://doi.org/10.1111/j.1095-8649.2007.01627.x.

Buechel, S.D., Boussard, A., Kotrschal, A., et al., 2018. Brain size affects performance in a reversal-learning test. Proc. R. Soc. B Biol. Sci. 285, 20172031. https://doi.org/10.1098/rspb.2017.2031.

Camacho-Alpízar, A., Guillette, L.M., 2023. From whom do animals learn? A meta-analysis on model-based social learning. Psychon. Bull. Rev. 30, 863–881. https://doi.org/10.3758/s13423-022-02236-4.

Castro, L., Wasserman, E.A., 2014. Pigeons' tracking of relevant attributes in categorization learning. J. Exp. Psychol. Anim. Learn Cogn. 40, 195–211. https://doi.org/10.1037/xan0000022.

Choleris, E., Kavaliers, M., 1999. Social Learning in Animals: Sex Differences and Neurobiological Analysis. Pharmacol. Biochem. Behav. 64, 767–776. https://doi.org/10.1016/S0091-3057(99)00141-0.

Choleris, E., Valsecchi, P., Wang, Y., et al., 1998. Social learning of a food preference in male and female mongolian gerbils is facilitated by the anxiolytic, chlordiazepoxide. Pharmacol. Biochem. Behav. 60, 575–584. https://doi.org/10.1016/S0091-3057(98)00005-7.

Culbert, B.M., Talagala, S., Barnett, J.B., et al., 2020. Context-dependent consequences of color biases in a social fish. Behav. Ecol. 31, 1410–1419. https://doi.org/10.1093/beheco/araa099.

Culbert, B.M., Tsui, N., Balshine, S., 2021. Learning performance is associated with social preferences in a group-living fish. Behav. Process. 191, 104464. https://doi.org/10.1016/j.beproc.2021.104464.

van de Waal, E., Renevey, N., Favre, C.M., Bshary, R., 2010. Selective attention to philopatric models causes directed social learning in wild vervet monkeys. Proc. R. Soc. B Biol. Sci. 277, 2105–2111. https://doi.org/10.1098/rspb.2009.2260.

Desjardins, J.K., Fitzpatrick, J.L., Stiver, K.A., et al., 2008. Costs and benefits of polygyny in the cichlid *Neolamprologus pulcher*. Anim. Behav. 75, 1771–1779. https://doi.org/10.1016/j.anbehav.2007.09.037.

Dierkes, P., Heg, D., Taborsky, M., et al., 2005. Genetic relatedness in groups is sex-specific and declines with age of helpers in a cooperatively breeding cichlid. Ecol. Lett. 8, 968–975. https://doi.org/10.1111/j.1461-0248.2005.00801.x.

Dugatkin, L.A., Godin, J.J., 1997. Reversal of female mate choice by copying in the guppy (Poecilia reticulata). Proc. R. Soc. Lond. Ser. B Biol. Sci. 249, 179–184. https://doi.org/10.1098/rspb.1992.0101.

Dunlap, A.S., Papaj, D.R., Dornhaus, A., 2017. Sampling and tracking a changing environment: persistence and reward in the foraging decisions of bumblebees. Interface Focus 7, 20160149. https://doi.org/10.1098/rsfs.2016.0149.

Félix, A.S., Oliveira, R.F., 2021. Integrative neurobiology of social behavior in cichlid fish. In: Abate, M.E., Noakes, D.L.G. (Eds.), The Behavior, Ecology and Evolution of Cichlid Fishes. Springer Netherlands, Dordrecht, pp. 637–681.

Figueroa, J., Solà-Oriol, D., Manteca, X., Pérez, J.F., 2013. Social learning of feeding behaviour in pigs: Effects of neophobia and familiarity with the demonstrator conspecific. Appl. Anim. Behav. Sci. 148, 120–127. https://doi.org/10.1016/j.applanim.2013.06.002.

Fischer, S., Balshine, S., Hadolt, M.C., Schaedelin, F.C., 2021. Siblings matter: Family heterogeneity improves associative learning later in life. Ethology 127, 897–907. https://doi.org/10.1111/eth.13196.

Friard, O., Gamba, M., 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods in ecology and evolution 7 (11), 1325–1330.

Frostman, P., Sherman, P.T., 2004. Behavioral response to familiar and unfamiliar neighbors in a territorial cichlid, Neolamprologus pulcher. Ichthyol. Res 51, 283–285. https://doi.org/10.1007/s10228-004-0223-9.

Fuss, T., Flöck, S., Witte, K., 2021. Sex-specific cognitive flexibility in Atlantic mollies when learning from male demonstrators exploring a new food source. Anim. Behav. 173, 9–19. https://doi.org/10.1016/j.anbehav.2020.12.012.

Galef, B.G., Laland, K.N., 2005. Social learning in animals: empirical studies and theoretical models. BioScience 55, 489–499. https://doi.org/10.1641/0006-3568(2005)055[0489:SLIAES]2.0.CO;2.

Galef, B.G., Whiskin, E.E., 2008. Effectiveness of familiar kin and unfamiliar nonkin demonstrator rats in altering food choices of their observers. Anim. Behav. 76, 1381–1388. https://doi.org/10.1016/j.anbehav.2008.07.004.

Guadagno, A., Triki, Z., 2024. Executive functions and brain morphology of male and female dominant and subordinate cichlid fish. Brain Behav. 14 (5), e3484.

Hick K., Reddon A.R., O'Connor C.M., Balshine S., 2014. Strategic and tactical fighting decisions in cichlid fishes with divergent social systems. https://doi.org/10.1163/1568539X-00003122.

Heg, D., Taborsky, M., 2010. Helper response to experimentally manipulated predation risk in the cooperatively breeding cichlid Neolamprologus pulcher. PLoS One 5 (5), e10784.

Hellmann, J.K., Ligocki, I.Y., O'Connor, C.M., Reddon, A.R., Garvy, K.A., Marsh-Rollo, S. E., Hamilton, I.M., 2015. Reproductive sharing in relation to group and colony-level attributes in a cooperative breeding fish. Proceedings of the Royal Society B: Biological Sciences 282 (1811), 20150954.

Hotta, T., Takeyama, T., Jordan, L.A., Kohda, M., 2014. Duration of memory of dominance relationships in a group living cichlid. Naturwissenschaften 101, 745–751. https://doi.org/10.1007/s00114-014-1213-z.

Jordan, A., Taborsky, B., Taborsky, M., 2021. Cichlids as a model system for studying social behaviour and evolution. In: Abate, M.E., Noakes, D.L.G. (Eds.), The Behavior, Ecology and Evolution of Cichlid Fishes. Springer Netherlands, Dordrecht, pp. 587–635.

Jordan, L.A., Wong, M.Y.L., Balshine, S.S., 2009. The effects of familiarity and social hierarchy on group membership decisions in a social fish. Biol. Lett. 6, 301–303. https://doi.org/10.1098/rsbl.2009.0732.

King, A.J., Fürtbauer, I., Mamuneas, D., et al., 2013. Sex-differences and temporal consistency in stickleback fish boldness. PLOS ONE 8, e81116. https://doi.org/10.1371/journal.pone.0081116.

Kohda, M., Jordan, L.A., Hotta, T., et al., 2015. Facial recognition in a group-living cichlid fish. PLOS ONE 10, e0142552. https://doi.org/10.1371/journal.pone.0142552.

La Loggia, O., Rüfenacht, A., Taborsky, B., 2022. Fish can infer relations between colour cues in a non-social learning task. Biol. Lett. 18, 20220321. https://doi.org/10.1098/rsbl.2022.0321.

Laland, K.N., 2004. Social learning strategies. Learn. Behav. 32, 4–14. https://doi.org/10.3758/BF03196002.

Laland, K.N., Williams, K., 1998. Social transmission of maladaptive information in the guppy. Behav. Ecol. 9, 493–499. https://doi.org/10.1093/beheco/9.5.493.

Laland, K.N., Brown, C., Krause, J., 2003. Learning in fishes: from three-second memory to culture. Fish Fish 4, 199–202. https://doi.org/10.1046/j.1467-2979.2003.00124.x.

Laland, K.N., Atton, N., Webster, M.M., 2011. From fish to fashion: experimental and theoretical insights into the evolution of culture. Philos. Trans. R. Soc. Lond. B Biol. Sci. 366, 958–968. https://doi.org/10.1098/rstb.2010.0328.

Latchem, E., Brown, C., Balshine, S., 2025. The influence of social rank on learning in a group-living fish. Anim. Behav. 226, 123246. https://doi.org/10.1016/j.anbehav.2025.123246.

Le Vin, A.L., Mable, B.K., Arnold, K.E., 2010. Kin recognition via phenotype matching in a cooperatively breeding cichlid, *Neolamprologus pulcher*. Anim. Behav. 79, 1109–1114. https://doi.org/10.1016/j.anbehav.2010.02.006.

Lee, V.E., Thornton, A., 2021. Animal cognition in an urbanised world. Front Ecol. Evol. 9. https://doi.org/10.3389/fevo.2021.633947.

Lucon-Xiccato, T., Bisazza, A., 2014. Discrimination reversal learning reveals greater female behavioural flexibility in guppies. Biology Letters 10 (6), 20140206.

Lucon-Xiccato, T., Bisazza, A., Pilastro, A., 2019. Exploratory behaviour covaries with preference for unfamiliar males in female guppies. Anim. Behav. 155, 217–224. https://doi.org/10.1016/j.anbehav.2019.07.009.

Manning, A, Dawkins, MS, 2012. Learning and memory. In: *An Introduction to Animal Behaviour*, 6th ed. Cambridge University Press, Cambridge, pp. 239–276.

Munch, K.L., Noble, D.W.A., Wapstra, E., While, G.M., 2018. Mate familiarity and social learning in a monogamous lizard. Oecologia 188, 1–10. https://doi.org/10.1007/s00442-018-4153-z.

Nityananda, V., 2016. Attention-like processes in insects. Proc. R. Soc. B Biol. Sci. 283, 20161986. https://doi.org/10.1098/rspb.2016.1986.

Pongrácz, P., Miklósi, Á., Kubinyi, E., et al., 2003. Interaction between individual experience and social learning in dogs. Anim. Behav. 65, 595–603. https://doi.org/10.1006/anbe.2003.2079.

Ramakers, J.J.C., Dechmann, D.K.N., Page, R.A., O'Mara, M.T., 2016. Frugivorous bats prefer information from novel social partners. Anim. Behav. 116, 83–87. https://doi.org/10.1016/j.anbehav.2016.03.021.

Rymer, T., Schradin, C., Pillay, N., 2008. Social transmission of information about novel food in two populations of the African striped mouse, Rhabdomys pumilio. Anim. Behav. 76, 1297–1304. https://doi.org/10.1016/j.anbehav.2008.06.014.

Salena M. (2020) Comparative cognition between social and non-social cichlids. McMaster University.

Salena, M.G., Balshine, S., 2020. Social memory and quantity discrimination: a cross cichlid species comparison. Can. J. Exp. Psychol. 74, 207–214. https://doi.org/10.1037/cep0000212.

Sarin, S., Dukas, R., 2009. Social learning about egg-laying substrates in fruitflies. Proc. R. Soc. B Biol. Sci. 276, 4323–4328. https://doi.org/10.1098/rspb.2009.1294.

Schürch, R., Heg, D., 2010. Life history and behavioral type in the highly social cichlid Neolamprologus pulcher. Behav. Ecol. 21, 588–598. https://doi.org/10.1093/beheco/arq024.

Shettleworth, S.J., 2001. Animal cognition and animal behaviour. Anim. Behav. 61, 277–286. https://doi.org/10.1006/anbe.2000.1606.

Stanbrook, E., Jodoin, J., Culbert, B., et al., 2020. Learning Performance Is Influenced by the Social Environment in Cichlid Fishes. Can. J. Exp. Psychol. 74, 215–227. https://doi.org/10.1037/cep0000236.

Stiver, K.A., Dierkes, P., Taborsky, M., Balshine, S., 2004. Dispersal patterns and status change in a co-operatively breeding cichlid Neolamprologus pulcher: evidence from microsatellite analyses and behavioural observations. J. Fish. Biol. 65, 91–105. https://doi.org/10.1111/j.0022-1112.2004.00427.x.

Stiver, K.A., Dierkes, P., Taborsky, M., et al., 2005. Relatedness and helping in fish: examining the theoretical predictions. Proc. R. Soc. B Biol. Sci. 272, 1593–1599. https://doi.org/10.1098/rspb.2005.3123.

Stiver, K.A., Fitzpatrick, J., Desjardins, J.K., Balshine, S., 2006. Sex differences in rates of territory joining and inheritance in a cooperatively breeding cichlid fish. Anim. Behav. 71, 449–456. https://doi.org/10.1016/j.anbehav.2005.06.011.

Stiver, K.A., Desjardins, J.K., Fitzpatrick, J.L., et al., 2007. Evidence for size and sex-specific dispersal in a cooperatively breeding cichlid fish. Mol. Ecol. 16, 2974–2984. https://doi.org/10.1111/j.1365-294X.2007.03350.x.

Taborsky, B., Arnold, C., Junker, J., Tschopp, A., 2012. The early social environment affects social competence in a cooperative breeder. Anim. Behav. 83, 1067–1074. https://doi.org/10.1016/j.anbehav.2012.01.037.

Taborsky, M., 2016. Cichlid fishes: a model for the integrative study of social behavior. In: Koenig, W.D., Dickinson, J.L. (Eds.), Cooperative Breeding in Vertebrates, 1st edn. Cambridge University Press, pp. 272–293.

Thünken, T., Hesse, S., Bakker, T.C.M., Baldauf, S.A., 2016. Benefits of kin shoaling in a cichlid fish: familiar and related juveniles show better growth. Behav. Ecol. 27, 419–425. https://doi.org/10.1093/beheco/arv166.

Valvo, J.J., Rodd, F.H., Hughes, K.A., 2019. Consistent female preference for rare and unfamiliar male color patterns in wild guppy populations. Behav. Ecol. 30, 1672–1681. https://doi.org/10.1093/beheco/arz134.

Watson, S.K., Vale, G.L., Hopper, L.M., et al., 2018. Chimpanzees demonstrate individual differences in social information use. Anim. Cogn. 21, 639–650. https://doi.org/10.1007/s10071-018-1198-7.

Webster, M.M., Laland, K.N., 2010. Reproductive state affects reliance on public information in sticklebacks. Proc. R. Soc. B Biol. Sci. 278, 619–627. https://doi.org/10.1098/rspb.2010.1562.

Wong, M., Balshine, S., 2011. The evolution of cooperative breeding in the African cichlid fish, Neolamprologus pulcher. Biol. Rev. Camb. Philos. Soc. 86, 511–530. https://doi.org/10.1111/j.1469-185X.2010.00158.x.

Wong, M.Y.L., Jordan, L.A., Marsh-Rollo, S., et al., 2012. Mating systems in cooperative breeders: the roles of resource dispersion and conflict mitigation. Behav. Ecol. 23, 521–530. https://doi.org/10.1093/beheco/arr218.

R Core Team (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.