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The influence of social rank on learning in a group-living fish

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Dominance hierarchies are found in many group-living species, and an individual's social rank can influence their access to resources, behaviours and physiology. However, the effect of rank on learning capability has not been well studied. Here, we examined how rank influences learning in the group-living cichlid fish *Neolamprologus pulcher*. We tested learning in both dominant and subordinate fish and investigated whether rank is related to the capacity to learn independently as well as from others. Fish learned to move coloured discs to access a food reward, either by trial and error on their own, or by watching a trained demonstrator. We found no differences between ranks in the individual associative learning task, but subordinates were faster at changing their behaviour when we changed the reward rules (during the reversal learning phase). We also found no differences in the number of trials it took dominants and subordinates to socially learn the task (from watching demonstrators), but individuals learned the task faster when they could observe others. Our results indicate that some aspects of cognition can be influenced by social rank, but rank does not appear to affect general learning ability.

Social cohesion of group-living species often depends on individuals knowing their position within a dominance hierarchy. Typically, a few animals in a social group are the dominants while the rest are subordinate (Drews, 1993; Sapolsky, 2005) and usually, these different ranks reflect an animal's competitive abilities (Chase et al., 2002). The presence of the social hierarchy reduces internal competition and aggression within the group, as each individual knows where they belong in the pecking order (Tibbetts et al., 2022). Differences between social ranks have been well studied, and researchers have shown repeatedly and across taxa that dominant animals tend to be larger, more aggressive, have higher levels of androgens and more resources (Drews, 1993; Hemelrijk, 2000). Dominants are often more risk averse, possibly to avoid or minimize unnecessary risks that could jeopardize their social position (Herberholz et al., 2007). In contrast, subordinates tend to be smaller, are often more stressed and more behaviourally flexible (Boogert et al., 2006; Drews, 1993; Filby et al., 2010; Gilmour et al., 2005; Katzir, 1982; Milewski et al., 2022; Stahl et al., 2001).

How an animal's rank impacts their learning capabilities is not well understood. One theory suggests dominants should be better learners, because subordinates often need to devote time and energy to avoid aggression, potentially suppressing their ability to learn (Griffin et al., 2013; Keynan et al., 2016; Overington et al., 2009). Better learners are also expected to be able to gain advantages that will allow them to climb through the ranks (Langley, van Horik, Whiteside, Beardsworth, & Madden, 2018; Seyfarth & Cheney, 2002). But another theory suggests the opposite: that because subordinates are weaker competitors, they will be unable to directly compete with dominants, making them more likely to come up with alternative solutions to problems and be the innovators within a social group (Bókony et al., 2014; Keynan et al., 2016; Reader & Laland, 2003). In general, subordinates are thought to be more behaviourally flexible and more willing to take on risks, as such risk-taking behaviour can help them to move up in rank or access additional resources; behavioural flexibility and risk taking are often associated with greater cognition and learning capabilities (Chase et al., 2002; Langley, van Horik, Whiteside, Beardsworth, & Madden, 2018; Sih & Del Giudice, 2012).

Not only is there conflicting theory about how social rank might influence learning capability, the limited empirical research conducted to date on this topic has also produced mixed results (Langley, van Horik, Whiteside, & Madden, 2018). In some species, dominants are better learners (e.g. meadow voles, *Microtus pennsylvanicus*; house mice, *Mus musculus*; pheasants, *Phasianus colchicus*; European starlings, *Sturnus vulgaris*), while in other species, subordinates are better learners (e.g. zebra finches, *Taeniopygia*

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guttata; longtailed macaques, *Macaca fascicularis*) (Barnard & Luo, 2002; Barrett et al., 2022; Boogert et al., 2006; Bunnell et al., 1980; Fitchett et al., 2005; Langley, van Horik, Whiteside, & Madden, 2018). Furthermore, there are a number of studies where no observable differences in learning were detected between social ranks (e.g. domestic roosters, *Gallus gallus*; horses, *Equus caballus*; spotted hyaenas, *Crocuta crocuta*) (Benson-Amram & Holekamp, 2012; Christensen et al., 2012; Croney et al., 2007; Francia et al., 2006). However, the methods used to test learning have varied widely across these studies, which may be the cause of some of the discrepancies.

It is possible that, instead of one social rank always being the better learner, individuals of different ranks may simply be better at a particular type of learning. In general, animals learn in one of two ways: through their own experiences (known as asocial or individual learning) or by watching and copying others (known as social learning: Galef, 2009; Kendal et al., 2005). Social learning is less energetically costly but can also be unreliable, whereas individual learning is more reliable but comes with greater risks (Camacho-Alpízar & Guillette, 2023; Hoppitt & Laland, 2013; Munch et al., 2018). As subordinates tend to be behaviourally flexible, neophilic and risk prone (Seok An et al., 2011), we hypothesize that they should be better at the riskier individual learning. In particular, a subordinate's behavioural flexibility might allow them to excel at reversal learning, a test of cognitive flexibility where an individual has to change from responding to a previously learned stimulus to responding to a new stimulus to receive a reward (Fong et al., 2019; Izquierdo et al., 2017). In contrast, dominant animals that are typically more risk averse and less behaviourally flexible may be less likely to individually learn and might even prefer, when possible, to learn socially (Boogert et al., 2006; Laland, 2004). Differences in the propensity to socially learn may also depend on the relationship between the demonstrator and observer. A more dominant, older or trusted individual, for example, may make a better demonstrator either because it may provide more reliable information or attract more attention due to its social prestige (Camacho-Alpízar & Guillette, 2023; Pongrácz et al., 2008).

Much of the previous experimental research conducted on rank and learning has focused on birds and mammals, leaving major gaps in our knowledge about the relationship in other taxa. *Neolamprologus pulcher* is a group-living cichlid fish species endemic to Lake Tanganyika in Africa with social hierarchies made up of a dominant male and female pair, and up to 20 mixed-sex subordinates (Balshine et al., 2001; Wong & Balshine, 2011). *Neolamprologus pulcher* have highly stable ranks, with dominant members typically holding their position for several months to a year (Stiver et al., 2004; Wong & Balshine, 2011) and clear behavioural differences between ranks (Culbert et al., 2019; Heg et al., 2004; Ruberto et al., 2020; Wong & Balshine, 2011). There are also differences in brain morphology between individual *N. pulcher* of different social rank (Guadagno & Triki, 2024). While these authors also tested for reversal learning, as we did in this study (see below), they used a different methodology and investigated asocial learning but not social learning. We expected subordinates to take fewer trials to learn asocially, particularly when reversal learning. We expected that dominants would socially learn more quickly. For the reasons outlined above, we also expected both dominant and subordinate observers to learn faster from dominant demonstrators in the social learning trials.

METHODS

The experiments described below were conducted at the Aquatic Behavioural Ecology Laboratory at McMaster University between January and November 2023 using laboratory-reared *N. pulcher*. Prior to the experiments, the fish were held in 189-litre social tanks in long-term groups of four to six fish. Groups were socially stable and had been kept together for at least 4 months before the start of the procedures outlined below. All social group aquaria were maintained at 26–28 °C, on a 12:12 h light:dark cycle. Fish were observed daily, and we monitored their ranks and health. Fish were fed ad libitum 6 days a week with commercial fish flakes. Prior to beginning each experiment, the fish were sexed and measured for their standard length (in mm) and mass (to 0.01 g). The social rank of each fish was determined by behavioural observations (Sopinka et al., 2009), with the largest male and female in each social group being the dominants. In total, 10 different social groups were used for the asocial learning experiments and 25 different social groups were used in the social learning experiment.

Learning Assay

Fish were trained over a series of trials to move either a small blue or yellow coloured plastic disc (2 cm in diameter) off a feeding tray, following the procedure developed by Lucon-Xiccato and Bisazza (2014) and tested in *N. pulcher* by Culbert et al. (2021). Whenever the fish moved a disc, they were able to access a food reward (a small piece of bloodworm, approximately 5 mm long). The feeding tray was a white plastic rectangular block (2 × 10 × 5 cm) with 10 small upward-facing shallow holes or food wells. Each well was 0.9 cm in diameter and 0.5 cm deep (see Results, Figs. 1a and 2a). In the first trials, to familiarize the fish with the apparatus, we placed the disc next to a well containing food. As the fish learned to eat from the wells, we moved the disc, so it covered more and more of the well on each ensuing trial (starting with covering 25% of the well, then 50%, then 75% and finally 100%). This meant the fish had to eventually move the disc to access the food reward. Fish typically took 5–10 trials to learn to move a disc that was fully covering the food reward and an additional 10 trials to solidify their performance and consistently move the disc. If re-enforcement training was needed (i.e. for demonstrators in experiment 2), we conducted these re-enforcement trials using a similar process as described here but began the trials with the disc already half covering the well. The well that was baited and covered on the feeding tray was always chosen at random, using a random number generator (numbergenerator.org). This learning/foraging assay was selected because it is simple to learn and it mimics behaviours such as moving stones and sand that are commonly performed by the *N. pulcher* in the wild and in the laboratory (Balshine et al., 2001; Culbert et al., 2021; Naef & Taborsky, 2020).

Experiment 1: Asocial (Individual) Learning

This experiment was conducted between 25 January and 22 May 2023. Thirty-four fish (17 dominants and 17 subordinates) were taken from their respective social group tanks and placed individually into a learning tank (see Results, Fig. 1a), such that each learning tank housed only one fish. The learning tanks were 38-litre tanks (50 × 27 × 31 cm), split into two sections by a movable opaque barrier. The front section of the tank contained a feeding tray, and the back section contained a half clay flowerpot that each fish could use as shelter. All tanks were fitted with a mechanical water filter, maintained at 26–28 °C and had approximately 2 cm of crushed coral sand as substrate.

Phase 1: initial learning

Fish were given 24 h to acclimatize to their new tank. After the acclimatization period, each fish was given 1 h to explore the feeding tray (see below) before being trained over a series of trials

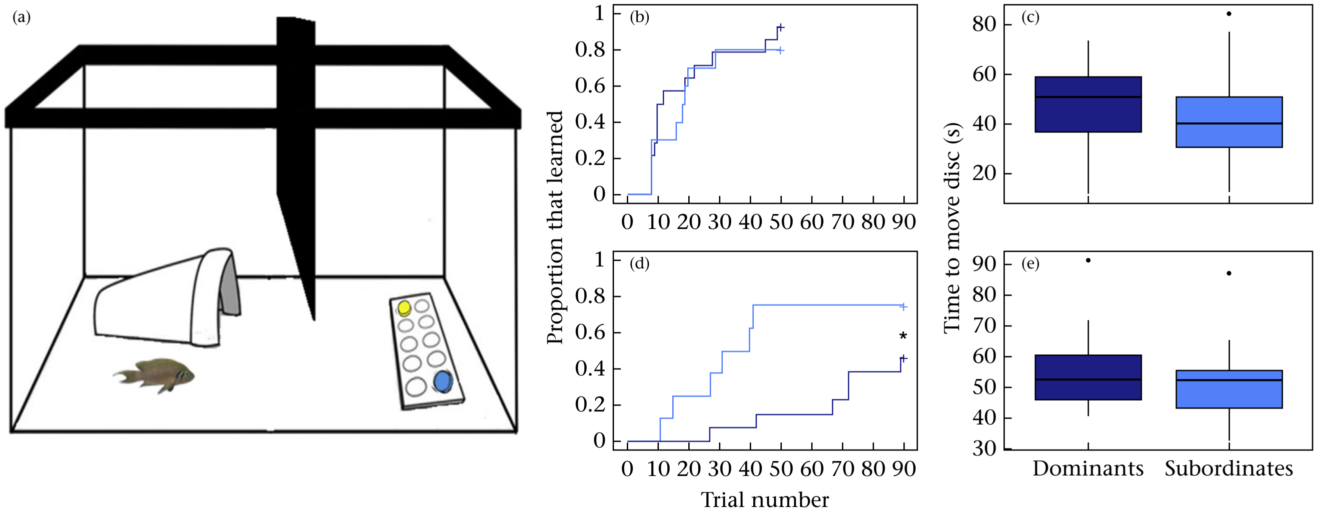

Figure 1. (a) Illustration of the individual learning tanks and social control tanks. Survivorship curves showing the number of trials required to learn (b) the associative learning task and (d) the reversal learning task. Latencies to move the disc in (c) the associative learning trials and (e) the reversal learning trials. Dominant *N. pulcher* are represented by dark blue; subordinate *N. pulcher* are represented by light blue.

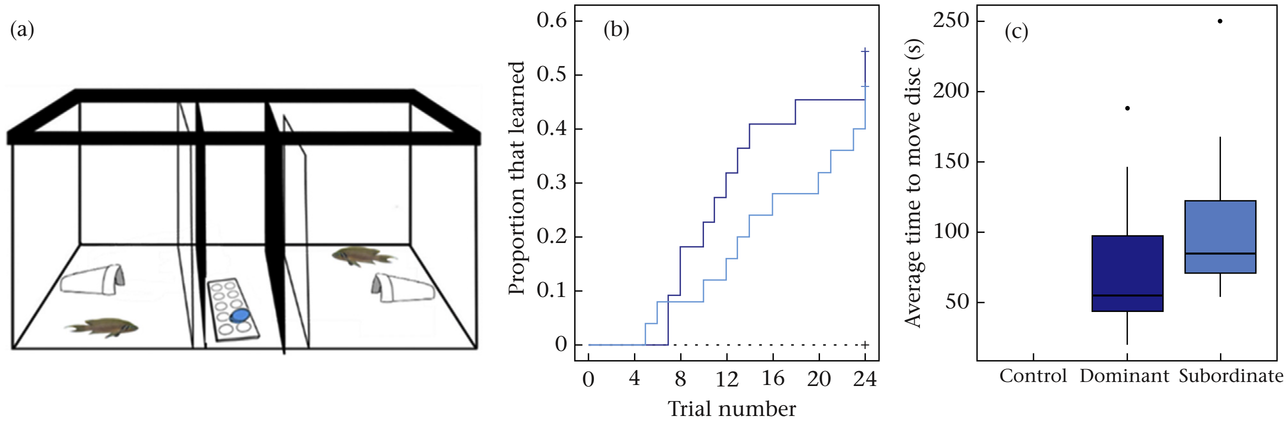

Figure 2. (a) An illustration of the social learning tank. (b) Survivorship curve showing the number of trials to learn the social learning task. (c) Latency to move the disc in the social learning trials. Control fish are represented by the black dotted line in (b); dominant *N. pulcher* are represented by dark blue and subordinates are represented by light blue in both (b) and (c).

to move a single coloured plastic disc, as explained above. During each trial, the opaque barrier was lifted, allowing the fish to access and interact with the feeding tray, the plastic disc and the food reward. Fish were given 2 min to move the disc and/or eat the food. Regardless of whether the fish moved the disc and ate the food reward, we gently guided each fish back to its clay shelter after 2 min and lowered opaque barrier, allowing us to reset and rebait the feeding tray without disturbing the fish. The fish typically interacted with the food reward and disc quickly and returned to their shelters on their own. Half the fish were trained to move a blue disc and half the fish were trained to move a yellow disc. At this point there was only one disc per trial. We ran 10 trials per day for a maximum of 5 days (i.e. a maximum of 50 trials per fish). Ten fish (three dominants and seven subordinates) failed to learn to move the disc from a fully covered well and were excluded from the associative and reversal learning trials.

Phase 2: associative learning

Once a fish had moved a disc from a fully covered well in three consecutive trials, we began the associative learning trials where a second disc was added. The new disc was the alternative colour (either blue or yellow) from the colour the fish had originally learned to move, and this 'incorrect' disc had a stainless-steel nut attached to the bottom, with the nut fitting snuggly into the feeding well and preventing the fish from lifting or moving the disc. A food reward was placed under both the 'correct' movable disc and the 'incorrect' immovable disc. Trials continued until the fish always interacted and moved the correct disc (the colour they had originally learned to move) in eight out of 10 consecutive trials (binomial test: $P = 0.04$). For the associative phase of the experiment, we ran 10 trials per day for a maximum of 5 days. Three fish (one dominant and two subordinates) failed to reach our learning criterion and were excluded from the reversal learning trials.

Phase 3: reversal learning

Once a fish reached the learning criteria, we commenced the reversal learning phase of the experiment. If a fish did not learn (did not reach the learning threshold of eight out of 10 correct) at the associative phase, it was excluded from the reversal learning task. In the reversal learning trials, we switched which coloured disc was movable, forcing the fish to suppress their previous colour training and learn to make a new colour choice to receive a food reward.

Because this is considered a more challenging task, we ran 10 trials per day for up to 9 days in this reversal phase of the experiment (i.e. a maximum of 90 trials per fish). Again, the fish were considered to have reached the reversal learning criteria if they successfully moved the correct coloured disc in eight out of 10 consecutive trials. All trials (associative and reversal phase trials) were recorded on a Sony FDR-AX700 camcorder (set to record at 4000 and 30 frames/s) set up in front of the learning tanks.

Experiment 2: Social Learning

This experiment was conducted between 28 April and 10 November 2023. The social learning tanks were 70-litre tanks (76 × 30.5 × 30.5 cm) divided into three compartments by two sets of movable plastic barriers (each set of barriers included one opaque and one clear PVC barrier). The two outer compartments each contained a half clay pot shelter while the centre compartment contained the feeding tray (see Results, Fig. 2a). The tanks also contained 2 cm of coral sand substrate, an aquarium heater, an airstone and a mechanical filter and were maintained at 26–28 °C throughout the experiment. A demonstrator fish (a fish that had previously been trained to move either a yellow or a blue coloured disc) was placed on one side of the social learning tank and a naïve observer fish was added to the other side. An equal number of dominant and subordinate demonstrators ($N = 24$ of each) were used in this experiment. Half of the demonstrator and observer pairs came from the same social group (were familiar with each other) while half came from different social groups (and were unfamiliar with each other).

Phase 1: demonstrator testing

Demonstrators were given 24 h to acclimatize to their new tanks, then tested to confirm they would consistently move a disc that fully covered a well to get a food reward. If a demonstrator did not move the disc consistently (three trials in a row), they were retrained following the methodology described above. Once all demonstrators were consistently moving the disc, we added a naïve observer fish to each social learning tank in the opposite outer compartment. Apart from during the demonstration, the demonstrator and observer could not see each other as they were separated between trials by two opaque and two clear barriers. In total, there were 22 same-rank demonstrator–observer pairings (dominant demonstrators with dominant observers or subordinate demonstrators with subordinate observers) and 26 mixed-rank demonstrator–observer pairings (dominant–subordinate and subordinate–dominant combinations). Observer fish were always given 24 h to acclimatize to the new tank, then given 1 h to explore the middle compartment with an empty feeding tray. During this acclimation period the observer fish could not see the demonstrator fish.

Phase 2: observer trials

We then ran five demonstrator trials in a row, followed by a single observer trial. During the demonstrator trials, we raised both barriers on the demonstrator's side and the opaque barrier on the observer's side. This allowed the observer fish to see the demonstrator and watch the demonstrator move the disc to reach the food reward. The clear PVC barrier prevented the observer from entering the middle compartment and directly interacting with either the demonstrator or the feeding tray. After allowing the observer to watch the five demonstrator trials, we ran one observer trial. During the observer trial, both barriers on the observer's side were raised, but both barriers on the demonstrator's side were down. This allowed the observer to interact with the disc and the feeding tray but fully blocked the demonstrator fish from view and prevented any potential social distractions. We repeated this process twice per day, approximately 1 h apart, for a total of 10 demonstrator trials and two observer trials per day for each observer–demonstrator pair of fish. Discs always fully covered the food. Trials ran until the observers had moved the disc in three consecutive trials or for a maximum of 12 days (i.e. up to a maximum of 24 observer trials per fish). If the demonstrator failed to move the disc during one of their demonstration trials, that trial was rerun immediately. If the demonstrator failed again to move the disc (failed in two consecutive trials), we ended that set of trials for the day. One demonstrator completely stopped moving the disc halfway through the experiment, so we excluded that demonstrator–observer pair from our analysis. Observers were given a maximum of 24 trials due to time restraints on the facility where the social learning tanks were housed and to prevent the observer fish from eventually learning to move the disc asocially.

Phase 3: control trials

To ensure that the observers were indeed copying the behaviours of the demonstrators and not simply learning to move the disc by themselves, we also ran control trials with 18 naïve fish, nine dominants and nine subordinates. These 18 control fish neither saw any demonstrators nor had the task demonstrated for them. They were placed individually into the asocial learning tanks (see Results, Fig. 1a) without any demonstrator to show them how to lift the disc. Just like the observer fish in the social learning experiment, control fish were given 24 h to acclimatize to the tank, plus 1 h to explore the empty feeding tray, before the control trials began. Each control fish was randomly assigned to a disc colour, resulting in an equal number of fish learning on blue and yellow discs. In each control trial, food was placed in a random well and then fully covered by the disc. Each control fish was given two trials per day (just like the observer fish) to try and move the disc. Trials ran for a total of 12 days (24 trials per fish in total) or until the fish moved the disc in three consecutive trials. All control and social trials were recorded on an Sony FDR-AX700 (with the same settings as above) and placed in front of the tank on a tripod.

Behavioural Assays

Behavioural traits such as boldness, exploration, activity and sociality have been found to affect aspects of cognition across a wide range of taxa (Dougherty & Guillette, 2018). To control for any potential differences in these behavioural traits across social rank, we ran a series of behavioural assays before conducting the learning trials. Within 4 days of beginning the learning trials, focal fish were tested using two behavioural assays. One assay tested for activity, exploration and boldness, and the second assay tested sociality. The order of these behavioural assays was randomized for each fish by flipping a coin.

Activity and exploration in an open-field assay

Activity and exploration were tested by placing an individual focal fish into a large, novel behavioural tank (96 × 46 × 43 cm) that had the back, front and one side covered with blue adhesive paper to prevent any potential distractions from outside the tank. The bottom of the tank was a simple glass bottom, with a 5 × 5 cm grid drawn on it. The water temperature in the tank was maintained at 26–28 °C and a half clay flowerpot was placed at one end of the arena, which served as a shelter and starting place for the fish. To begin this assay, a focal fish was taken from its group tank and gently placed inside the clay flowerpot with the entrance of the pot blocked by a movable clear plastic barrier. The barrier prevented the fish from exiting the flowerpot and we left the barrier in place for 5 min. After 5 min, the plastic barrier was lifted, allowing the fish to exit the shelter if it desired and freely swim around the tank for 10 min. Across the tank from the shelter there was a movable opaque barrier, behind which was a Kendall's lamprologus, *Lepidiolamprologus kendalli*, a predator of *N. pulcher*, that was housed in a separate tank to avoid any olfactory cues. After the initial 10 min, we lifted the opaque barrier to reveal the *L. kendalli* for an additional 10 min.

The exploration, activity and the predator response phases of the trial were all recorded by a camera (Sony FDR-AX700, with the same settings as above) mounted above the aquarium. We scored the time it took the fish to leave the shelter and how much time each fish spent in the shelter in the first 10 min of the trial. We also recorded the total number of gridlines crossed by each fish and the number of unique gridlines crossed by each fish in the first 10 min of the trial. We then divided the number total number of gridlines the fish crossed by the amount of time the fish spent outside of the shelter to get a measure of activity. We recorded the time the fish spent near the walls of the tank (a measure of thigmotaxis) and in the central grids. This last measure was based on classic open-field tests that measure thigmotaxis (staying close to vertical surfaces), which is thought to be an antipredator defence strategy (Lamprea et al., 2008). Finally, we measured the time the focal fish spent near the predator in the second 10 min of the trials, when the predator could be seen. Focal fish were considered to be near the predator when they were in the grid square closest to the predator.

Sociality assay

Sociality was tested on all focal fish in a different but identical 96 × 46 × 43 cm glass tank, split into three identical compartments (each compartment was 32 × 46 × 43 cm in size). The compartments were separated by a clear unmovable barrier and by an opaque movable barrier. In this assay, a previously established social group was placed in one of the end compartments, while the opposite tank compartment was left empty. The social group consisted of two dominants and one subordinate that were unknown to the focal fish, and the side on which the social group was placed (left versus right) was randomly assigned by flipping a coin. The middle compartment was separated into four, 8 cm wide sections by drawing vertical lines on the front of the tank. At the start of this assay, each focal fish was placed individually in a clear tube in the middle compartment for a 5 min acclimation period. The two opaque barriers and the plastic tube were then remotely lifted, allowing the focal fish to see both outer compartments and to swim freely around the middle compartment. Trials lasted for 10 min and were recorded on a Sony FDR-AX700 set up on a tripod in front of the tank. We measured the proportion of time that the focal fish spent within one grid space (approximately one body length, 8 cm) of the social group.

Video Scoring

All the videos were scored by research assistants who remained blind to the rank identity of the focal fish. In each learning trial, we recorded whether the focal fish moved the disc, the total number of times the disc was moved throughout the trial (frequency of interaction) and the time it took to move the disc (latency to interaction). In the social learning experiment, we also recorded the total number of interactions fish had with the feeding tray, the time each fish spent in the centre compartment and any interactions that occurred between the demonstrator and the focal fish (e.g. ramming or biting the clear barrier). For both experiments, we considered anytime the fish touched the 'incorrect' disc or tried to eat out of an empty well as a 'mistake' and scored these as well. In total, we scored 2823 asocial trials and 1815 social trials. Although a small percentage of trials were lost due to video camera or memory card technical issues ($N = 88$, 0.03% of the asocial trials; $N = 31$, 0.02% of the social learning trials), we took notes after each trial so we could determine whether the discs had been moved.

Statistical Analysis

All data analyses were conducted using R (version 4.3.3), with an α set to 0.05. We initially analysed the influence of social rank on learning performance using a mixed effects Cox proportional hazards regression model ('Coxme' package in R). A Cox proportional regression model is a semiparametric model that does not make assumptions about the distributions of the response variables. Any individual that failed to reach its learning criteria (eight out of 10 trials in the asocial learning tasks or three moves in a row for the social learning task) were coded as censored observations. This allows us to avoid making assumptions about the learning capabilities of these individuals as they might have been able to learn if we had continued trials for longer.

To reduce the number of variables/behaviours that needed to be analysed, we conducted a principal components analysis (PCA) for the behavioural assays scored (the total number of lines crossed, the number of unique lines crossed, the time spent in the shelter, the time it took fish to leave the shelter, the time spent in the centre grids, the time spent near the predator and the time spent near the social group) using the 'FactorMineR' package in R. All behavioural scores were mean-centred and standardized before being used in the PCA with the 'scale' function in R (Schielzeth, 2010). After performing the PCA, we used a Cattell–Nelson–Gorsuch (CNG) scree test (using the 'nFactors' package in R) to determine how many principal components to keep. The CNG scree test is a more objective version of the commonly used technique of visually inspecting a scree plot (Gorsuch & Nelson, 1981). Using this more objective method, we determined that it would be appropriate to include the first three principal components for both experiments. All principal components had an eigenvalue ≥ 1.

We used separate models to examine how social rank influenced success on the associative, reversal and social learning tasks as well as the initial training task, using the number of trials to reach the learning criteria as the response variable, the focal fish's social rank as a predictor variable and the social tank the fish came from as a random effect. We also wanted to know whether the inclusion of sex, the first three principal components and the dominance rank and/or sex of the demonstrator fish would improve the fit of the models. We also included disc colour as a potential variable in our models, but we did not find that disc colour had any effect on the number of trials it took fish to learn (Latchem et al., 2023). To find the best-fitting model, we used the 'dredge' function ('MuMIn' package in R) to test a set of models with all combinations of variables. This function produces scores for Akaike's information criterion corrected for small samples (AICc) for all possible models. We then chose the best-fitting model that included the rank predictor variable. A reduction of the AICc score by at least 2 was treated as a better model, and if multiple models differed by a score of 2 or less, we chose to use the model with the fewest variables to avoid overfitting.

To test for proportional hazards in our models, we visually inspected the Schoenfeld residuals against the transformed number of trials that it took the fish to learn. This analysis plots the covariate value for an individual that failed to learn, minus the individual's estimated value, assuming our sample had proportional hazards across all trials, which allowed us to test whether the hazard rate across our trials was constant. We then used a DFBETA residual plot to check for any influential observations, with any DFBETA residual ≥ 1 being considered an influential observation

(Xue & Schifano, 2017). We did not find any violations of the Cox proportional hazards model assumptions in our models.

As only a small sample of fish successfully achieved reversal learning, we conducted an additional simpler analysis (an unpaired two-sample *t* test) to confirm the findings of the Cox models. We used a Shapiro test to confirm normality and attempted to normalize any non-normal data with a log transformation. All groups met the assumption of equal variance. If the data could not be normalized, we used a Wilcoxon two-sample test as a nonparametric alternative. As it was not guaranteed that observers who were unfamiliar with their demonstrators would be able to correctly ascertain the social rank of the demonstrator, we also tested to see whether there was a correlation between the relative size differences between the observers and demonstrators (based on mass) and the number of trials taken to socially learn. We then tested whether being familiar with the demonstrator (if they came from the same original social group) would make it more likely for the observers to learn using a chi-square test.

After testing for the effect of the behavioural tendencies of the focal fish (via PCA) on learning and on how the rank of the demonstrators influenced learning (number of trials until the fish consistently moved the correct disc), we analysed whether there was a correlation between the number of trials it took fish to learn and the time it took to move a disc or the number of mistakes it made. We also tested whether there was a difference in the number of mistakes made by dominants versus subordinates and whether learning speed was correlated with the number of times the demonstrator fish moved the disc, the time it took the demonstrator to move the disc or the number of mistakes the demonstrator made.

Ethical Note

All procedures in this study were approved by the University of McMaster Animal Care Committee (AUP: 22-03-09). During the learning trials, fish were monitored daily for welfare. Following the completion of the learning trials, all fish were returned to their social tanks and to their original social groups. We typically tested all the members of a social group at the same time and returned individuals at the same time to their social home tank. Social groups were carefully monitored for aggression when individuals were returned, and although the fish interacted more upon reintroduction, no obvious signs of distress were observed and normal levels of social behaviours were restored typically within a 1−2 h.

RESULTS

Experiment 1: Asocial Learning

Initial training

We found that 24 of our 34 fish were able to consistently move the disc during our initial training phase. In total, 14 dominants and 10 subordinates learned the simple training task of moving a disc to get a food reward. Dominants took a mean (± SE) of 22.2 ± 3.3 trials to learn this task, while subordinates took 15.3 ± 3.6 trials to learn to consistently move the disc. We did not find a significant effect of rank on the number of trials it took fish to learn to move the disc (mixed effects Cox proportional hazards model: hazards ratio $= 0.69$, $z = -0.81$, $P = 0.42$). Note that the same result was revealed when we conducted a *t* test on the data (Cohen's $d = 0.56$, unpaired *t* test: $t_{22} = 1.72$, $P = 0.10$).

Associative learning phase

In the associative learning phase, 21 of our 24 fish learned to move the correct disc. Fish took an average (± SE) of 17.3 ± 2.6 trials to learn to move the correct disc, with dominant ($N = 13$) fish learning the associative task in 18.3 ± 3.9 trials and subordinates ($N = 8$) taking 15.8 ± 2.6 trials to learn. The model of best fit for the associative learning task included the second principal component (PC2), which we thought of as sociality because the time spent near the social group loaded most strongly on this principal component. We found no significant effect of either social rank (mixed effects Cox proportional hazards model: hazards ratio $= 0.64$, $z = -0.92$, $P = 0.36$; Fig. 1b) or PC2 (hazards ratio $= 1.33$, $z = 1.34$, $P = 0.18$) on the number of trials it took the fish to associatively learn. We did not find any behavioural traits (based on the PCAs) that were significantly correlated with the number of trials it took to associatively learn (Supplementary Figs. S1a, b, c). This result was again found using a simpler test (Cohen's $d = 0.20$, Wilcoxon two-sample test: $W = 55$, $N = 21$, $P = 0.85$).

Reversal learning phase

Only fish that successfully reached the associative learning criteria advanced to the reversal learning trials. The reversal learning criteria was only met by 12 of the 21 fish (six of each social rank). Overall, fish took 44.1 ± 7.3 trials to reverse the task they had previously learned, taking more than double the number of trials (i.e. 17.3 ± 2.6) that it took fish to master the initial associative task. Dominants ($N = 6$) took significantly longer (more trials) to learn the reversal task (60.8 ± 9.4 trials) compared with subordinates ($N = 6$, 27.3 ± 5.1; mixed effects Cox proportional hazards model: hazard ratio $= 3.27$, $z = 2.01$, $P = 0.045$; Fig. 1d). Again, a similar result was revealed when we performed a simple *t* test (Cohen's $d = 1.8$, unpaired *t* test: $t_{10} = 3.1$, $P = 0.01$). None of the behavioural tendencies (PCAs) were correlated with the number of trials it took to achieve reversal learning (Supplementary Figs. S1d, e, f).

Experiment 2: Social Learning

Learning from others to move a disc and reaching the social learning criteria of moving a disc three times in a row was met by only 51% of the fish (24/47, 13 dominants and 11 subordinates). However, none of the control fish (0/18) were able to successfully learn to move the disc consistently. Of the fish that learned, 14 were familiar with their demonstrators (i.e. were originally from the same social group) and 10 were unfamiliar (from different social groups). Familiarity with the demonstrator did not increase the likelihood that observers would learn (chi-squared test: $\chi^2 = 0.53$, $P = 0.47$). There was no improvement to the model with the addition of any other variables (sex, behaviour, etc.). Naïve dominant (13.2 ± 1.7 trials) and naïve subordinate (16.3 ± 1.9) observers did not differ in the number of trials taken to socially learn to move the disc (mixed effects Cox proportional hazards model: hazard ratio $= 0.77$, $z = -0.63$, $P = 0.53$; see Fig. 2b). The rank of the demonstrator also did not have an effect on the trials taken to learn (hazard ratio $= 0.78$, $z = -0.61$, $P = 0.55$). Also, the relative size difference between the demonstrator and the observer and the number of trials taken to learn were not clearly related (Spearman's rank correlation: $r_S = 0.24$, $S = 1750.1$, $P = 0.26$).

Behavioural Assays

Asocial learning PCA

The behavioural traits scored for the fish in the asocial learning trials loaded strongly on three principal components, which together explained 74% of the total variance (see Table 1 for the contributions and loadings of each behaviour). PC1 explained 39.1% of the total variation, PC2 explained 19.1% and PC3 explained 15.7%. PC1 increased as the fish crossed more unique gridlines and spent less time in the shelter. Thus, we considered PC1 to be a measure of

Table 1

Average behavioural scores measured for the fish in the asocial learning trials and loadings of each behaviour on the three principal components (PCs) used in our analysis

	Time near social group (s)	Lines crossed per min	Unique lines crossed	Time in centre grids (s)	Time near predator (s)	Time in shelter (s)	Time to leave shelter (s)
Mean ± SE	370±23.16	7.1±0.97	9.7±1.5	87±15.6	118.4±25.1	251.8±40.1	182.3±44.6
PC1 (Exploration) contribution %	0.63	13.68	**28.54**	13.63	6.66	**27.23**	9.6
PC1 loading strength	−0.07	0.36	**0.53**	0.36	0.25	**−0.52**	0.30
PC2 (Sociality) contribution %	**50.59**	5.29	3.05	3.77	18.91	8.23	10.13
PC2 loading strength	**0.71**	−0.23	−0.17	0.19	0.43	−0.28	−0.32
PC3 (Boldness) contribution %	7.68	25.19	4.58	2.75	**29.29**	0.31	**30.19**
PC3 loading strength	0.27	0.50	0.21	0.17	**−0.54**	0.05	**−0.55**

PC1 had an eigen value of 2.7, PC2 had and eigen value of 1.3 and PC3 had an eigen value of 1.1. The ‘contribution %’ reflects the variables’ percentage of contribution to each principal component. The loading strength explains the correlation and direction (positive or negative) of each variable for each principal component. The main variables contributing to each principal component are shown in bold.

exploration. PC2 increased as the fish spent more time near the social group, so we considered PC2 to be a measure of sociality. PC3 was driven by the time the fish spent near the predator and the time taken to leave the shelter, and so we considered PC3 to be a measure of boldness. We did not find a significant difference in PC1, PC2 or PC3 between ranks (see Supplementary Table S1).

Social learning PCA

The first three principal components were also included in our results for the social learning experiment (see Table 2 for the contributions and loadings). In this second experiment, PC1 explained 42.3% of the total variation, PC2 explained 19.3% of the total variation and PC3 explained 13.1% of the total variation. We found that the first three principal components for the social learning experiment had similar loadings to the results found in the asocial learning experiment. As in the asocial learning experiment, PC1 increased as the fish crossed more unique gridlines and as the fish spent less time in the shelter. So once again, we considered PC1 to be a measure of exploration. PC2 increased as the fish spent more time near the social group, so PC2 was again considered to be a representation of sociality. We found that PC3 increased as time spent in the centre grids increased and as the time to leave shelter decreased. So, we considered PC3 to be a measure of boldness. We did not find a significant difference in PC1, PC2 or PC3 between ranks (see Supplementary Table S2).

Latency to Move the Disc, Number of Mistakes and Demonstrator Behaviours

Latency to move the disc

During the associative learning phase, fish took an average (± SE) of 46.4 ± 4.1 s to move the correct disc (see Fig. 1c). The time taken to move the correct disc was not significantly correlated with how quickly the fish associatively learned (Spearman’s rank correlation: $r_S = 0.33$, $S = 1035.4$, $P = 0.15$). Fish took a little longer on average to move the correct disc during the reversal learning trials (54.5 ± 3.0 s; see Fig. 2e), and again there was no significant correlation between the time to move the correct disc and the number of trials to learn in the reversal learning task ($r_S = -0.35$, $S = 387.18$, $P = 0.25$). Fish in the social learning trials took the longest to move the disc during their trials, with a mean of 90.77 ± 11.7 s before moving the disc (see Fig. 2c).

Number of mistakes

In the associative phase of the individual learning experiment, fish interacted with the wrong disc or an incorrect well an average of 2.6 ± 1.1 times per trial. There was no difference in the number of mistakes made by each rank (Cohen’s $d = 0.64$, unpaired t test: $t_{19} = -1.5$, $P = 0.10$). We did not find any correlation between the number of mistakes made and how quickly fish learned in the associative phase (Spearman’s rank correlation: $r_S = -0.19$, $S = 1841.5$, $P = 0.40$). Fish made the most mistakes during the reversal learning phase, with a mean of 4.4 ± 0.6 mistakes per trial. Dominant fish made fewer mistakes (3.5 + 0.7) than subordinates (5.6 + 0.8; Cohen’s $d = 0.56$, t test: $t_{10} = -2.18$, $P = 0.04$). However, the number of mistakes that a fish made during the reversal learning trials was not significantly correlated with how many trials it took the fish to learn the reversal task (Spearman’s rank correlation: $r_S = -0.46$, $S = 419.23$, $P = 0.12$). In the social learning experiments, fish made ‘mistakes’ (i.e. interacted with an incorrect well) an average of 0.4 ± 0.1 per trial. Once again, the number of mistakes was not significantly correlated with the number of trials it took observers to socially learn ($r_S = 0.05$, $S = 2462.3$, $P = 0.80$).

Demonstrator behaviours

Demonstrators moved the disc on average after 22.4 ± 2.2 s. We did not find any correlation between the time demonstrators took to move the disc and the number of trials it took observers to learn ($r_S = -0.19$, $S = 2748.6$, $P = 0.36$). Demonstrators interacted with the disc frequently during the demonstrator trials, moving the disc

Table 2

Average behavioural scores measured for the fish in the social learning trials and loadings of each behaviour on the three principal components (PCs) used in our analysis

	Time near social group (s)	Lines crossed per min	Unique lines crossed	Time in centre grids (s)	Time near predator (s)	Time in shelter (s)	Time to leave shelter (s)
Mean ± SE	401.6±22	7.62±2.2	7.52±1	51.1±9.7	117.6±17.7	359.5±30.6	361.7±47.7
PC1 (Exploration) contribution %	1.28	7.83	**26.68**	12.3	17.81	**27.46**	6.6
PC1 loading strength	0.11	0.27	**0.51**	−0.35	−0.42	**−0.52**	0.25
PC2 (Sociality) contribution %	**41.89**	36.36	0.97	5.4	0.54	0.71	14.12
PC2 loading strength	**0.64**	0.6	0.09	−0.23	0.07	0.08	0.37
PC3 (Boldness) contribution %	0.01	9.54	1.12	**46.78**	9.54	0.17	**41.95**
PC3 loading strength	−0.013	−0.06	0.1	**0.68**	−0.31	−0.04	**−0.64**

PC1 had an eigen value of 2.95, PC2 had and eigen value of 1.35 and PC3 had an eigen value of 1.0. The ‘contribution %’ reflects the variables’ percentage of contribution to each principal component. The loading strength explains the correlation and direction (positive or negative) of each variable for each principal component. The main variables contributing to the principal components are shown in bold.

an average of 3.2 ± 0.2 times in each trial. We found that observers took longer (more trials) to learn the more times their demonstrator moved the disc ($r_S = 0.50$, $S = 1140.7$, $P = 0.01$).

DISCUSSION

In this study we tested how social rank influenced learning capabilities in the group-living fish species *N. pulcher*. We expected subordinates to be faster asocial learners and dominants to be faster social learners. We also expected that all fish would socially learn faster from a dominant demonstrator. We found that social rank did not influence the number of trials it took fish to learn to move a disc to get a food reward or to learn to associate the correct coloured disc to a food reward. However, subordinate fish were able to reverse their learned colour preferences faster than the dominants (reversal learning). We also found that dominants and subordinates took a similar number of trials to learn to access a food reward when learning from others. Contrary to expectation, the rank of the demonstrator did not influence the number of trials it took observers to learn the socially learned task.

Our findings suggest that social rank influences cognitive flexibility but not learning in *N. pulcher*. Reversal learning is thought to be a test of cognitive flexibility, a form of executive function (Diamond, 2013; Montalbano et al., 2022), and not a test of learning. Cognitive flexibility is the ability of an animals to change or adapt behaviours to better fit a situation (Fong et al., 2019; Tello-Ramos et al., 2019). Subordinate animals are often more behaviourally flexible (Drews, 1993; Katzir, 1982; S. Reader & Laland, 2001; Stahl et al., 2001) as they need to respond to the behaviour of other group members. Subordinate *N. pulcher* are behaviourally flexible as they modify their helping behaviour and their position in the territory based on their size relative to the dominant (Hamilton et al., 2005). Subordinate *N. pulcher* can also leave their natal groups and join new groups to increase their social status (Balshine et al., 2001; Heg et al., 2004; Reddon et al., 2011; Stiver et al., 2007). Better reversal learning capacity may be important in allowing the subordinates to quickly adapt to changes in both their natal groups as well as their new groups.

Inhibitory control is another executive function that has commonly been associated with reversal learning (Izquierdo & Jentsch, 2012). Inhibitory control is a measure of an animal's ability to inhibit a response or behaviour (Diamond, 2013). No difference in inhibition was found between social ranks when *N. pulcher* were tested with a standardized detour test (Guadagno & Triki, 2024). This suggests that the difference in reversal learning is due only to a difference in cognitive flexibility, and not due to inhibitory control. It should be noted that Guadagno and Triki (2024) also tested reversal learning and did not find a difference in performance based on social rank. However, these authors used a different learning assay, in which the *N. pulcher* were rewarded whenever they swam close to a coloured disc, and the fish did not directly interact with the disc.

Our results suggest that *N. pulcher* have some cognitive plasticity. Cognitive plasticity in animals is a rapidly growing field. Cognitive flexibility, tested through reversal learning trials, has been found to be plastic in multiple different species. For example, guppies, *Poecilia reticulata*, reared with predator cues were better at reversal learning tasks than those raised without predator cues (Montalbano et al., 2022). Both house mice, *Mus musculus*, and Norway rats, *Rattus norvegicus*, show increased performance on reversal learning tasks when raised in enriched environments (Braun et al., 2019; Zeleznikow-Johston et al., 2017). Cognitive flexibility can also vary with age. Older domestic dogs, *Canis lupus familiaris*, have been shown to perform worse in reversal learning tests than younger dogs (Mongillo et al., 2013; Piotti et al., 2018). More direct tests of the plasticity of cognitive flexibility in *N. pulcher* in relation to age and the degree of environment enrichment could yield interesting results.

Contrary to the commonly held expectation that dominant animals are better social learners (van Boekholt et al., 2021), we found that dominant and subordinate fish needed a similar number of trials to socially learn. However, parallel results have been found in other species, including in black-capped chickadees, *Poecile atricapillus* (Seok An et al., 2011). A possible explanation for our results is that dominants and subordinates in our artificial laboratory conditions had equal social learning opportunities. Often in wild social groups, dominants control social learning opportunities by displacing other members of the group, as has been found in chacma baboons, *Papio ursinus* (Carter et al., 2016). It is possible that if tested within a group (a more ecologically relevant situation for *N. pulcher*), the social dynamics of the group could result in rank differences in social learning.

Surprisingly, fish were equally likely to learn the social learning task irrespective of the social rank of the demonstrator. We expected that all observers would learn faster from dominant demonstrators, as dominants are often older, larger fish with more resources and hence can be seen as more reliable sources of information (Camacho-Alpízar & Guillette, 2023; Pongrácz et al., 2008; van Schaik, 2010). However, a bias towards learning from dominants is not universal among animals. Norway rats copy the food choices of subordinate demonstrators (Awazu & Fujita, 1998, 2000), and wild vervet monkeys, *Chlorocebus aethiops*, of different rank show no bias towards learning (Botting et al., 2018). Again, this would be worth retesting in a social group setting.

We also found that only 51% of the fish socially learned, a much lower frequency than expected given that *N. pulcher* commonly use the same behaviours (e.g. lifting and carrying) required to learn the task. As none of the control fish learned to move the disc in a similar timeframe, it does seem that learning performance was enhanced by observing conspecifics perform the task. So why did only half of our observers learn? One possibility is that, in our laboratory experiments, observers may have had little motivation to move the discs. Territory maintenance behaviour is energetically costly (Grantner & Taborsky, 1998) and is typically performed as payment to be allowed in the dominant's territory (Balshine et al., 2001; Fischer et al., 2014; Naef & Taborsky, 2020). The discs and feeding tray were placed in a separate central compartment that the observers may not have considered part of their territory or subterritory (Werner et al., 2003), and as there were no group members around to assist or to impress, the observer may not have been motivated to interact with the learning apparatus. Low motivation has been shown to decrease learning in a different African cichlid fish, the *Astatotilapia burtoni* (Wood et al., 2011).

We did not find any correlation between the behavioural traits tested (such as activity, exploration, boldness or sociality) and learning. Our findings match the findings of a recent meta-analysis of personality and cognition, which showed that although personality is often studied for its effect on learning, there does not seem to be any general correlations between personality and learning capabilities (Dougherty & Guillette, 2018). *Neolamprologus pulcher* that switched their preference from a large group to a small group in the presence of a predator, perhaps as a way to avoid detection by predators, were faster learners (Culbert et al., 2021). In our behavioural set-up, the predator and sociality assays were separate, so we did not measure how risk might be modulated by sociality. We predicted that sociality might influence social learning tendency, but we did not find any evidence that this was the case. Webster (2023) suggested that social learning and sociality are not inherently linked. For example, aggressive juvenile Atlantic salmon, *Salmo salar*, which are nonsocial, can nevertheless learn socially

(Brown & Laland, 2002). *Neolamprologus pulcher* are also highly social fish, and it is possible that, by not allowing them to directly interact with their demonstrator, we masked any differences in social preferences between individuals.

One recurring limitation of studying learning in relation to social rank is that the fish had to be removed from their social groups to be tested. In the wild, *N. pulcher* have very stable social ranks within permanent social groups, with dominants and subordinates showing obvious behavioural and physiological differences (Aubin-Horth et al., 2007; Buchner et al., 2004; Culbert et al., 2018, 2024). Testing fish outside their social groups removed any potential impact that group dynamics might have on learning (Griffin et al., 2013; Keynan et al., 2016; Overington et al., 2009). By removing the potential for aggression from the dominants, subordinates may pay more attention and be able to learn better. It remains possible that more learning differences between ranks might be observed if the fish were tested while remaining in their own social groups. It is also possible that the impact of social interactions could be tested for by having the observers remain in visual contact with other group members while they learn to move the disc.

In conclusion, we found that social rank can influence certain aspects of cognition in the group-living fish *N. pulcher*. Specifically, we found that subordinate *N. pulcher* took fewer trials to achieve reversal learning in a foraging assay compared to dominant fish, but there were no differences between social ranks in a simple associative learning task or in a social learning task. These findings help us better understand how different individuals in the group can learn and adapt to changes in their environments. The differences in cognition that we uncovered were observed when individuals were isolated from their social group, and it is possible that stronger differences would arise, especially in social learning, if individuals were studied within the confines of their natural state, within their social group.

Author Contributions

Elias Latchem: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Culum Brown:** Writing – review & editing, Supervision, Conceptualization. **Sigal Balshine:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Data Availability

Supporting data is hosted by Zenodo and is available at https://doi.org/10.5281/zenodo.15002859.

Declaration of Interest

The authors have no declarations.

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Supplementary Material

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References

Aubin-Horth, N., Desjardins, J. K., Martei, Y. M., Balshine, S., & Hofmann, H. A. (2007). Masculinized dominant females in a cooperatively breeding species. *Molecular Ecology, 16*(7), 1349–1358. https://doi.org/10.1111/j.1365-294X.2007.03249.x

Awazu, S., & Fujita, K. (1998). Influence of social relationships on food transmission in rats. *Japanese Journal of Animal Psychology, 48*(2), 183–190. https://doi.org/10.2502/janip.48.183

Awazu, S., & Fujita, K. (2000). Influence of dominance on food transmission in rats. *Japanese Journal of Animal Psychology, 50*(1), 119–123. https://doi.org/10.2502/janip.50.119

Balshine, S., Leach, B., Neat, F., Reid, H., Taborsky, M., & Werner, N. (2001). Correlates of group size in a cooperatively breeding cichlid fish (*Neolamprologus pulcher*). *Behavioral Ecology and Sociobiology, 50*(2), 134–140. https://doi.org/10.1007/s002650100343

Barnard, C. J., & Luo, N. (2002). Acquisition of dominance status affects maze learning in mice. *Behavioural Processes, 60*(1), 53–59. https://doi.org/10.1016/S0376-6357(02)00121-3

Barrett, L. P., Marsh, J. L., Boogert, N. J., Templeton, C. N., & Benson-Amram, S. (2022). Links between personality traits and problem-solving performance in zebra finches (*Taeniopygia guttata*). *Royal Society Open Science, 9*(6), Article 212001. https://doi.org/10.1098/rsos.212001

Benson-Amram, S., & Holekamp, K. E. (2012). Innovative problem solving by wild spotted hyenas. *Proceedings of the Royal Society B: Biological Sciences, 279*(1744), 4087–4095. https://doi.org/10.1098/rspb.2012.1450

Bókony, V., Lendvai, Á. Z., Vágási, C. I., Pătraş, L., Pap, P. L., Németh, J., Vincze, E., Papp, S., Preiszner, B., Seress, G., & Liker, A. (2014). Necessity or capacity? Physiological state predicts problem-solving performance in house sparrows. *Behavioral Ecology, 25*(1), 124–135. https://doi.org/10.1093/beheco/art094

Boogert, N. J., Reader, S. M., & Laland, K. N. (2006). The relation between social rank, neophobia and individual learning in starlings. *Animal Behaviour, 72*(6), 1229–1239. https://doi.org/10.1016/j.anbehav.2006.02.021

Botting, J., Whiten, A., Grampp, M., & van de Waal, E. (2018). Field experiments with wild primates reveal no consistent dominance-based bias in social learning. *Animal Behaviour, 136*, 1–12. https://doi.org/10.1016/j.anbehav.2017.11.025

Braun, M. D., Kisko, T. M., Witt, S. H., Rietschel, M., Schwarting, R. K., & Wöhr, M. (2019). Long-term environmental impact on object recognition, spatial memory and reversal learning capabilities in *Cacna1c*-haploinsufficient rats. *Human Molecular Genetics, 28*(24), 4113–4131.

Brown, C., & Laland, K. (2002). Social enhancement and social inhibition of foraging behaviour in hatchery-reared Atlantic salmon. *Journal of Fish Biology, 61*(4), 987–998. https://doi.org/10.1111/j.1095-8649.2002.tb01857.x

Buchner, A. S., Sloman, K. A., & Balshine, S. (2004). The physiological effects of social status in the cooperatively breeding cichlid *Neolamprologus pulcher*. *Journal of Fish Biology, 65*(4), 1080–1095. https://doi.org/10.1111/j.0022-1112.2004.00517.x

Bunnell, B. N., Gore, W. T., & Perkins, M. N. (1980). Performance correlates of social behavior and organization: Social rank and reversal learning in crab-eating macaques (M. fascicularis). *Primates, 21*(3), 376–388. https://doi.org/10.1007/BF02390467

Camacho-Alpízar, A., & Guillette, L. M. (2023). From whom do animals learn? A meta-analysis on model-based social learning. *Psychonomic Bulletin & Review, 30*(3), 863–881. https://doi.org/10.3758/s13423-022-02236-4

Carter, A. J., Ticó, M. T., & Cowlishaw, G. (2016). Sequential phenotypic constraints on social information use in wild baboons. *eLife, 5*, Article e13125. https://doi.org/10.7554/eLife.13125

Chase, I. D., Tovey, C., Spangler-Martin, D., & Manfredonia, M. (2002). Individual differences versus social dynamics in the formation of animal dominance hierarchies. *Proceedings of the National Academy of Sciences of the United States of America, 99*(8), 5744–5749. https://doi.org/10.1073/pnas.082104199

Christensen, J. W., Ahrendt, L. P., Lintrup, R., Gaillard, C., Palme, R., & Malmkvist, J. (2012). Does learning performance in horses relate to fearfulness, baseline stress hormone, and social rank? *Applied Animal Behaviour Science, 140*(1–2), 44–52. https://doi.org/10.1016/j.applanim.2012.05.003

Croney, C. C., Prince-Kelly, N., & Meller, C. L. (2007). A note on social dominance and learning ability in the domestic chicken (*Gallus gallus*). *Applied Animal Behaviour Science, 105*(1–3), 254–258. https://doi.org/10.1016/j.applanim.2006.05.001

Culbert, B. M., Balshine, S., & Gilmour, K. M. (2018). Physiological regulation of growth during social ascension in a group-living fish. *Physiological and Biochemical Zoology, 92*(2), 211–222.

Culbert, B. M., Gilmour, K. M., & Balshine, S. (2019). Stress axis regulation during social ascension in a group-living cichlid fish. *Hormones and Behavior, 103*, 121–128. https://doi.org/10.1016/j.yhbeh.2018.06.007

Culbert, B. M., Ligocki, I. Y., Salena, M. G., Wong, M. Y. L., Hamilton, I. M., Bernier, N. J., & Balshine, S. (2024). Social regulation of arginine vasopressin and oxytocin systems in a wild group-living fish. *Hormones and Behavior, 161*, Article 105521. https://doi.org/10.1016/j.yhbeh.2024.105521

Culbert, B. M., Tsui, N., & Balshine, S. (2021). Learning performance is associated with social preferences in a group-living fish. *Behavioural Processes, 191*, Article 104464. https://doi.org/10.1016/j.beproc.2021.104464

Diamond, A. (2013). Executive functions. *Annual Review of Psychology, 64*, 135–168.

Dougherty, L. R., & Guillette, L. M. (2018). Linking personality and cognition: A meta-analysis. *Philosophical Transactions of the Royal Society B: Biological Sciences, 373*(1756), Article 20170282. https://doi.org/10.1098/rstb.2017.0282

Drews, C. (1993). The concept and definition of dominance in animal behaviour. *Behaviour, 125*(3–4), 283–313. https://doi.org/10.1163/156853993X00290

Filby, A. L., Paull, G. C., Bartlett, E. J., van Look, K. J. W., & Tyler, C. R. (2010). Physiological and health consequences of social status in zebrafish (*Danio rerio*). *Physiology & Behavior, 101*(5), 576–587. https://doi.org/10.1016/j.physbeh.2010.09.004

Fischer, S., Zöttl, M., Groenewoud, F., & Taborsky, B. (2014). Group-size-dependent punishment of idle subordinates in a cooperative breeder where helpers pay to stay. *Proceedings of the Royal Society B: Biological Sciences, 281*(1789), Article 20140184. https://doi.org/10.1098/rspb.2014.0184

Fitchett, A. E., Collins, S. A., Barnard, C. J., & Cassaday, H. J. (2005). Subordinate male mice show long-lasting differences in spatial learning that persist when housed alone. *Neurobiology of Learning and Memory, 84*(3), 247–251. https://doi.org/10.1016/j.nlm.2005.08.004

Fong, S., Buechel, S. D., Boussard, A., Kotrschal, A., & Kolm, N. (2019). Plastic changes in brain morphology in relation to learning and environmental enrichment in the guppy (*Poecilia reticulata*). *Journal of Experimental Biology, 222*(10), Article jeb200402. https://doi.org/10.1242/jeb.200402

Francia, N., Cirulli, F., Chiarotti, F., Antonelli, A., Aloe, L., & Alleva, E. (2006). Spatial memory deficits in middle-aged mice correlate with lower exploratory activity and a subordinate status: Role of hippocampal neurotrophins. *European Journal of Neuroscience, 23*(3), 711–728. https://doi.org/10.1111/j.1460-9568.2006.04585.x

Galef, B. G. (2009). Strategies for social learning: Testing predictions from formal theory. *Advances in the Study of Behavior, 39*, 117–151.

Gilmour, K. M., DiBattista, J. D., & Thomas, J. B. (2005). Physiological causes and consequences of social status in salmonid fish. *Integrative and Comparative Biology, 45*(2), 263–273. https://doi.org/10.1093/icb/45.2.263

Gorsuch, R. L., & Nelson, J. (1981). CNG scree test: An objective procedure for determining the number of factors. In *Paper presented at the annual meeting of the Society for Multivariate Experimental Psychology*.

Grantner, A., & Taborsky, M. (1998). The metabolic rates associated with resting, and with the performance of agonistic, submissive and digging behaviours in the cichlid fish *Neolamprologus pulcher* (Pisces: Cichlidae). *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology, 168*(6), 427–433. https://doi.org/10.1007/s003600050162

Griffin, A. S., Lermite, F., Perea, M., & Guez, D. (2013). To innovate or not: Contrasting effects of social groupings on safe and risky foraging in Indian mynahs. *Animal Behaviour, 86*(6), 1291–1300. https://doi.org/10.1016/j.anbehav.2013.09.035

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

Hamilton, I. M., Heg, D., & Bender, N. (2005). Size differences within a dominance hierarchy influence conflict and help in a cooperatively breeding cichlid. *Behaviour, 142*(11–12), 1591–1613.

Heg, D., Bender, N., & Hamilton, I. (2004). Strategic growth decisions in helper cichlids. *Proceedings of the Royal Society B: Biological Sciences, 271*(Suppl. 6), S505–S508. https://doi.org/10.1098/rsbl.2004.0232

Hemelrijk, C. K. (2000). Towards the integration of social dominance and spatial structure. *Animal Behaviour, 59*(5), 1035–1048. https://doi.org/10.1006/anbe.2000.1400

Herberholz, J., Mccurdy, C., & Edwards, D. H. (2007). Direct benefits of social dominance in juvenile crayfish. *Biological Bulletin, 213*(1), 21–27. https://doi.org/10.2307/25066615

Hoppitt, W., & Laland, K. N. (2013). *Social learning: An introduction to mechanisms, methods, and models*. Princeton University Press.

Izquierdo, A., Brigman, J. L., Radke, A. K., Rudebeck, P. H., & Holmes, A. (2017). The neural basis of reversal learning: An updated perspective. *Neuroscience, 345*, 12–26. https://doi.org/10.1016/j.neuroscience.2016.03.021

Izquierdo, A., & Jentsch, J. D. (2012). Reversal learning as a measure of impulsive and compulsive behavior in addictions. *Psychopharmacology, 219*, 607–620.

Katzir, G. (1982). Relationships between social structure and response to novelty in captive jackdaws, *Corvus monedula* L. I. Response to novel space. *Behaviour, 81*, 231–263. https://doi.org/10.1163/156853982X00157

Kendal, R. L., Coolen, I., van Bergen, Y., & Laland, K. N. (2005). Trade-offs in the adaptive use of social and asocial learning. *Advances in the Study of Behavior, 35*, 333–379. https://doi.org/10.1016/S0065-3454(05)35008-X

Keynan, O., Ridley, A. R., & Lotem, A. (2016). Task-dependent differences in learning by subordinate and dominant wild Arabian babblers. *Ethology, 122*(5), 399–410. https://doi.org/10.1111/eth.12488

Laland, K. N. (2004). Social learning strategies. *Learning & Behavior, 32*(1), 4–14. https://doi.org/10.3758/BF03196002

Lamprea, M. R., Cardenas, F. P., Setem, J., & Morato, S. (2008). Thigmotactic responses in an open-field. *Brazilian Journal of Medical and Biological Research, 41*(2), 135–140. https://doi.org/10.1590/S0100-879X2008000200010

Langley, E. J. G., van Horik, J. O., Whiteside, M. A., Beardsworth, C. E., & Madden, J. R. (2018). The relationship between social rank and spatial learning in pheasants, *Phasianus colchicus*: Cause or consequence? *PeerJ, 2018*(11), Article e5738. https://doi.org/10.7717/peerj.5738

Langley, E. J. G., van Horik, J. O., Whiteside, M. A., & Madden, J. R. (2018). Group social rank is associated with performance on a spatial learning task. *Royal Society Open Science, 5*(2), Article 171475. https://doi.org/10.1098/rsos.171475

Latchem, E., Culum, B., & Balshine, S. (2023). *Measuring the effects of blue and yellow on the number of trials to learn for* Neolamprologus pulcher*. Unpublished raw data*.

Lucon-Xiccato, T., & Bisazza, A. (2014). Discrimination reversal learning reveals greater female behavioural flexibility in guppies. *Biology Letters, 10*(6), Article 20140206. https://doi.org/10.1098/rsbl.2014.0206

Milewski, T. M., Lee, W., Champagne, F. A., & Curley, J. P. (2022). Behavioural and physiological plasticity in social hierarchies. *Philosophical Transactions of the Royal Society B: Biological Sciences, 377*(1845), Article 20200443.

Mongillo, P., Araujo, J. A., Pitteri, E., Carnier, P., Adamelli, S., Regolin, L., & Marinelli, L. (2013). Spatial reversal learning is impaired by age in pet dogs. *Age, 35*, 2273–2282.

Montalbano, G., Bertolucci, C., & Lucon-Xiccato, T. (2022). Cognitive phenotypic plasticity: Environmental enrichment affects learning but not executive functions in a teleost fish, *Poecilia reticulata*. *Biology (Basel), 11*(1), Article 64. https://doi.org/10.3390/biology11010064

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), 1–10. https://doi.org/10.1007/s00442-018-4153-z

Naef, J., & Taborsky, M. (2020). Commodity-specific punishment for experimentally induced defection in cooperatively breeding fish. *Royal Society Open Science, 7*(2), Article 191808. https://doi.org/10.1098/rsos.191808

Overington, S. E., Cauchard, L., Morand-Ferron, J., & Lefebvre, L. (2009). Innovation in groups: Does the proximity of others facilitate or inhibit performance? *Behaviour, 146*(11), 1543–1564. https://doi.org/10.1163/156853909X450131

Piotti, P., Szabó, D., Bognár, Z., Egerer, A., Hulsbosch, P., Carson, R. S., & Kubinyi, E. (2018). Effect of age on discrimination learning, reversal learning, and cognitive bias in family dogs. *Learning & Behavior, 46*, 537–553.

Pongrácz, P., Vida, V., Bánhegyi, P., & Miklósi, Á. (2008). How does dominance rank status affect individual and social learning performance in the dog (*Canis familiaris*)? *Animal Cognition, 11*(1), 75–82. https://doi.org/10.1007/s10071-007-0090-7

Reader, S. M., & Laland, K. N. (2001). Primate innovation: Sex, age and social rank differences. *International Journal of Primatology, 22*(5), 787–805. https://doi.org/10.1023/A:1012069500899

Reader, S. M., & Laland, K. N. (Eds.). (2003). *Animal innovation*. Oxford University Press.

Reddon, A. R., Balk, D., & Balshine, S. (2011). Sex differences in group-joining decisions in social fish. *Animal Behaviour, 82*(2), 229–234. https://doi.org/10.1016/j.anbehav.2011.04.017

Ruberto, T., Talbot, J. L., & Reddon, A. R. (2020). Head up displays are a submission signal in the group-living daffodil cichlid. *Behavioural Processes, 181*, Article 104271. https://doi.org/10.1016/j.beproc.2020.104271

Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. *Science, 308*(5722), 648–652.

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution, 1*(2), 103–113.

Seok An, Y., Kriengwatana, B., Newman, A. E., MacDougall-Shackleton, E. A., & MacDougall-Shackleton, S. A. (2011). Social rank, neophobia and observational learning in black-capped chickadees. *Behaviour, 148*(1), 55–69. https://doi.org/10.1163/000579510X545829

Seyfarth, R. M., & Cheney, D. L. (2002). What are big brains for? *Proceedings of the National Academy of Sciences of the United States of America, 99*(7), 4141–4142. https://doi.org/10.1073/pnas.082105099

Sih, A., & Del Giudice, M. (2012). Linking behavioural syndromes and cognition: A behavioural ecology perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*(1603), 2762–2772. https://doi.org/10.1098/rstb.2012.0216

Sopinka, N. M., Fitzpatrick, J. L., Desjardins, J. K., Stiver, K. A., Marsh-Rollo, S. E., & Balshine, S. (2009). Liver size reveals social status in the African cichlid *Neolamprologus pulcher*. *Journal of Fish Biology, 75*(1), 1–16.

Stahl, J., Tolsma, P. H., Loonen, M. J. J. E., & Drent, R. H. (2001). Subordinates explore but dominants profit: Resource competition in high Arctic barnacle goose flocks. *Animal Behaviour, 61*(1), 257–264. https://doi.org/10.1006/anbe.2000.1564

Stiver, K. A., Desjardins, J. K., Fitzpatrick, J. L., Neff, B., Quinn, J. S., & Balshine, S. (2007). Evidence for size and sex-specific dispersal in a cooperatively breeding cichlid fish. *Molecular Ecology, 16*(14), 2974–2984. https://doi.org/10.1111/j.1365-294X.2007.03350.x

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. *Journal of Fish Biology, 65*(1), 91–105. https://doi.org/10.1111/j.0022-1112.2004.00427.x

Tello-Ramos, M. C., Branch, C. L., Kozlovsky, D. Y., Pitera, A. M., & Pravosudov, V. V. (2019). Spatial memory and cognitive flexibility trade-offs: To be or not to be flexible, that is the question. *Animal Behaviour, 147*, 129–136.

Tibbetts, E. A., Pardo-Sanchez, J., & Weise, C. (2022). The establishment and maintenance of dominance hierarchies. *Philosophical Transactions of the Royal Society B: Biological Sciences, 377*(1845), Article 20200450. https://doi.org/10.1098/rstb.2020.0450 van Boekholt, B., van de Waal, E., & Sterck, E. H. (2021). Organized to learn: The influence of social structure on social learning opportunities in a group. *iScience, 24*(2), Article 102117. https://doi.org/10.1016/j.isci.2021.102117

van Schaik, C. P. (2010). Social learning and culture in animals. In P. Kappeler (Ed.), *Animal behaviour: Evolution and mechanisms* (pp. 623—653). Springer.

Webster, M. M. (2023). Social learning in non-grouping animals. *Biological Reviews (Cambridge), 98*(4), 1329—1344. https://doi.org/10.1111/brv.12954

Werner, N. Y., Balshine, S., Leach, B., & Lotem, A. (2003). Helping opportunities and space segregation in cooperatively breeding cichlids. *Behavioral Ecology, 14*(6), 749—756. https://doi.org/10.1093/beheco/arg067

Wong, M., & Balshine, S. (2011). The evolution of cooperative breeding in the African cichlid fish, *Neolamprologus pulcher. Biological Reviews (Cambridge), 86*(2), 511—530. https://doi.org/10.1111/j.1469-185X.2010.00158.x

Wood, L. S., Desjardins, J. K., & Fernald, R. D. (2011). Effects of stress and motivation on performing a spatial task. *Neurobiology of Learning and Memory, 95*(3), 277—285. https://doi.org/10.1016/j.nlm.2010.12.002

Xue, Y., & Schifano, E. D. (2017). Diagnostics for the Cox model. *Communications for Statistical Applications and Methods, 24*(6), 583—604.

Zeleznikow-Johnston, A., Burrows, E. L., Renoir, T., & Hannan, A. J. (2017). Environmental enrichment enhances cognitive flexibility in C57BL/6 mice on a touchscreen reversal learning task. *Neuropharmacology, 117*, 219—226.