

## Social Memory and Quantity Discrimination: A Cross Cichlid Species Comparison

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Cooperation is a highly complex social interaction that often requires coordination and communication between two individuals. Reciprocity is one explanation for how cooperation evolves and is maintained; help now will eventually be repaid in kind. For reciprocity to work, individuals must be able to differentiate between those who helped previously versus those who cheated. However, there is little empirical evidence that cooperative species have an enhanced recognition capacity compared to noncooperative species. Here we conducted a comparative study to address this question using three cooperatively breeding cichlids and three of their close relatives that are not cooperative breeders, all from Lake Tanganyika. In a first experiment, we offered fish a choice between spending time with a familiar versus an unfamiliar conspecific and found that while cooperative cichlids spent more time with familiar individuals, the noncooperative cichlids spent more time with unfamiliar individuals. In a second experiment, we provided a choice between affiliating with one versus three individuals (all unfamiliar) and found that 2/3 cooperative and 3/3 noncooperative cichlids strongly preferred to affiliate with larger groups. Our results suggest that both cooperative and noncooperative cichlids have evolved the ability to recognise familiar individuals and have affiliative preferences; however, the nature of these preferences differ.

### *Public Significance Statement*



Although the social intelligence hypothesis might suggest that the challenges of social life selected for enhanced cognitive abilities in group-living animals that cooperate, we show that both cooperatively breeding and noncooperative cichlid fishes have well-developed discrimination abilities. However, cooperatively breeding fishes preferred familiar individuals while noncooperative fishes did not. Hence our results support the notion that commonly encountered social challenges shape the brain and cognitive abilities.

*Keywords:* cognition, discrimination, familiarity, recognition, social memory

*Supplemental materials:* <http://dx.doi.org/10.1037/cep0000212.supp>

Cooperation is the act of working together toward a common goal, and its evolution can be challenging to explain because one party often appears to benefit at the cost of another (Axelrod &

Hamilton, 1981; Brosnan, Salwiczek, & Bshary, 2010; Nowak, 2006). Kin selection (indirect benefit) has traditionally been used to explain cooperation; where donors of costly help still benefit by

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The procedures used in this study were approved by the Animal Research Ethics Board of McMaster University (Animal Utilization protocol 18–04-16) and followed the guidelines established by the Canadian Council on Animal Care (CCAC) regarding the use of animals in research. We thank Adrienne McLean for her statistical wizardry and Avani Pathak for help with video scoring and elegant schematics. We would also like to thank Jeff Deminchuk, Nickolas Goenadi, Gheeda Mourtada, and Luke Brenton for their assistance with video scoring.

This work was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery grant to Sigal Balshine (RGPIN-2016–05772). Matthew G. Salena was supported by an Ontario Graduate Fellowship.

 The data are available at [https://osf.io/g34tk/?view\\_only=525d68e95db043849bc186668a7ac3f7](https://osf.io/g34tk/?view_only=525d68e95db043849bc186668a7ac3f7)

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having their relatives succeed (Hamilton, 1964; West, Griffin, & Gardner, 2007). More recently, many researchers have shifted their focus from indirect to direct benefits to explain the evolution of cooperation, where enhanced resource acquisition, survival, and reproduction are accrued via the cooperative act (Clutton-Brock, 2009; Leimar & Hammerstein, 2010; Taborsky, Frommen, & Riehl, 2016).

Cooperative breeding represents a complex form of cooperation that is observed in numerous mammals, birds, and insects (Arnold & Owens, 1999; Bernasconi & Strassmann, 1999; Koenig & Dickinson, 2004; Lacey & Sherman, 1997; Solomon & French, 1997). Cooperative breeding is characterised by alloparental care, where individuals help raise young that are not their own (Cornwallis, 2018). Although group-living and social interaction are common in fishes (Brown, Laland, & Krause, 2011), the Lamprologines of Lake Tanganyika, in Africa, are the only group of fishes that have evolved true cooperative breeding (Reddon et al., 2017; Taborsky, 2001; Tanaka et al., 2018). Within this tribe, cooperation has evolved independently, multiple times (Dey et al., 2017). The socio-cognitive challenges of living in a social group and cooperating to raise young are thought to have selected for particular cognitive abilities (Ashton, Ridley, Edwards, & Thornton, 2018; Croney & Newberry, 2007; Holekamp, 2007). For instance, living in a group and cooperating requires that individuals recognise, remember, and respond appropriately to their own group members versus strangers and invaders (Reddon et al., 2016). They must also find ways to quickly settle disputes (Balshine, Wong, & Reddon, 2017). Thus, discrimination between familiar and unfamiliar individuals is requisite to the maintenance of group cohesion and facilitates complex cooperative acts between group members; however, the extent to which noncooperative animals share this ability is still up for debate. This idea has not been tested in a comparative context, and further study will provide a deeper understanding of how cognitive ability has been molded by social challenges and the evolution of cooperation.

The use of fishes as models for studies of social cognition is becoming increasingly popular (Brown & Laland, 2003; Bshary, Gingins, & Vail, 2014; Vila Pouca & Brown, 2017). In this study, we examined differences in discrimination abilities (familiarity recognition and group-size assessment capability) between cooperative and noncooperative Lamprologine cichlids from Lake Tanganyika. These fishes exhibit remarkable diversity in their social propensity and behaviour (O'Connor, Marsh-Rollo, Ghio, Balshine, & Aubin-Horth, 2015; Seehausen, 2006; Sturmbauer, Salzburger, Duftner, Schelly, & Koblmüller, 2010; Taborsky, 2016). In our first experiment, we tested social memory and predicted that cooperative species would have better developed social memory, since they must be able to distinguish group members from nonmembers. We also predicted that, unlike the noncooperative species, the cooperative species would treat familiar individuals differently from strangers. Furthermore, based on results from two studies on Wistar rats (*Rattus norvegicus*) and zebrafish (*Danio rerio*), we predicted that cooperative cichlids would respond strongly to novelty, and spend more time investigating strangers versus familiar fish (Engelmann, Wotjak, & Landgraf, 1995; Madeira & Oliveira, 2017). In our second experiment, we tested quantity discrimination ability and predicted that cooperative cichlids would have superior quantity assessment capacity and grouping tendencies and show stronger preferences to affiliate

with groups, compared to closely related noncooperative cichlids. We expected cooperative species to outperform noncooperative species in the quantity discrimination task and spend more time grouping when presented with cues of predation risk. Our prediction is based on the observation that cooperatively breeding species live in groups for their entire lives and must overcome socio-cognitive challenges, like moderating aggressive tendencies, to accept and tolerate other sexually mature adults in their territories. However, we were also aware that a number of other studies have found similar quantitative capacities in more social and less social animals (Agrillo, Dadda, Serena, & Bisazza, 2008; Agrillo, Miletto Petrazzini, Tagliapietra, & Bisazza, 2012; Vonk & Beran, 2012).

## Materials and Methods

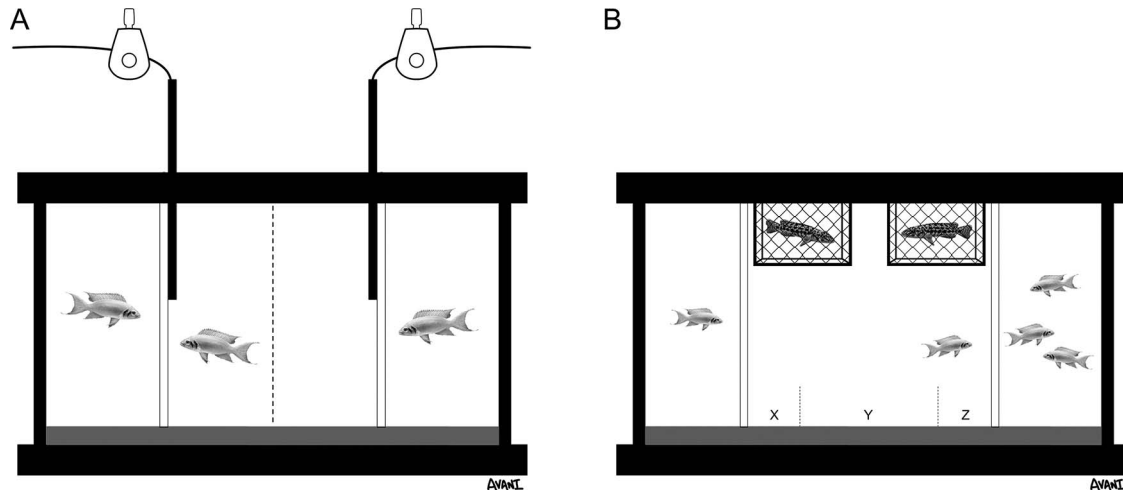
### Animals and Housing Conditions

Experiments were conducted between September 2018 and May 2019, using laboratory stocks of *Neolamprologus pulcher*, *Telmatochromis temporalis*, *Neolamprologus multifasciatus*, *Altolamprologus compressiceps*, *Julidochromis ornatus*, and *Neolamprologus tretocephalus* housed at McMaster University in Hamilton, Ontario, Canada. *N. pulcher*, *N. multifasciatus* and *J. ornatus* are cooperative breeders, whereas *T. temporalis*, *A. compressiceps*, and *N. tretocephalus* are noncooperative (Heg & Bachar, 2006; Heg, Bachar, & Taborsky, 2005; Mboko & Kohda, 1999; Nagoshi, 1983; Sefc, 2011; Taborsky, Brouwer, Heg, & Bachar, 2005). Each of these species are territorial (Awata, Heg, Munehara, & Kohda, 2006; Dey et al., 2017; Hick, Reddon, O'Connor, & Balshine, 2014; Nagoshi, 1983; Spreitzer, Mautner, Makasa, & Sturmbauer, 2012; Suriyampola & Eason, 2015). *N. pulcher* and *T. temporalis* were laboratory-reared descendants of wild-caught fishes from Lake Tanganyika, Africa. *N. multifasciatus*, *A. compressiceps*, *J. ornatus*, and *N. tretocephalus* were commercially bred and purchased from a local fish supplier (Finatics, Mississauga, Ontario, Canada). Fish were held in mixed-sex stock tanks fitted with filters, heaters, 2 cm of coral sand substrate, terracotta flowerpot halves, and opaque PVC tubes (10 cm in diameter and 25 cm in length) as shelter. Stock tanks were either 568-L tanks with ~60 individuals/tank or 189-L tanks with ~20 individuals/tank. These stock tanks and our experimental tanks (see below) were maintained at 25–28 °C and a 12L:12D photoperiod. Fish were fed six times per week ad libitum a diet of cichlid flakes and pellets.

### Experiment 1: Social Discrimination Task

Trials were conducted in 38-L (50 × 25 × 31 cm) aquaria that were well lit and fitted with a heater, a mechanical filter, and 2 cm of coral sand substrate. Each tank was lined with contact paper to minimise disturbance from neighbouring tanks. Tanks were divided into three compartments, by two fixed transparent barriers and two removable opaque barriers attached to a pulley system, allowing these barriers to be removed remotely (see Figure 1A).

**Day 1: Capture, measurement, and habituation.** Focal fish were captured from a stock tank, sexed, and measured (standard length and body mass) before being placed in the central compartment of an experimental tank. Then two size- and sex-matched unfamiliar conspecifics (see online supplemental materials for details) were selected from a different stock tank and were placed



**Figure 1.** (A) Experiment 1. Schematic of the aquaria used for the social discrimination task. Pulleys allowed opaque barriers to be lifted remotely, then the fish could interact across the fixed transparent barriers. The dashed line represents the divide by which preference was assessed. (B) Experiment 2. Schematic of the aquaria used for the quantity discrimination task. The dashed lines represent zones in the central compartment. The letters X and Z depict “choice” zones, while the letter Y depicts the neutral “no choice” zone.

in opposite end compartments (Figure 1A). All three fish were provided their own refuge (PVC tube) and left overnight in their respective chambers with removable opaque barriers and fixed transparent barriers between them.

**Day 2: Initial preference test.** The next day, refuges were removed, and the fish were left for 1h without shelter before the opaque partitions were lifted. Focal fish were then videotaped for 22 min and all interactions across the transparent barriers were recorded. After this period, opaque partitions were replaced, and one stimulus fish was randomly selected to remain in the test aquaria while the other was removed. The removed fish was replaced with another unfamiliar sex- and size-matched fish, again from a different stock tank, and all three fish had their refuges returned overnight.

**Day 3: Final test phase.** We repeated the identical procedure from Day 2 but now the focal fish was given an opportunity to interact with either a fish it had viewed the previous day (a familiar fish) or a fish it had never interacted with before (an unfamiliar fish). All interactions were videotaped for 22 min.

### Experiment 2: Quantity Discrimination Task

Following Experiment 1, focal fish were guided into a start box attached to a pulley (a PVC tube closed off at one end, with a sliding door at the other end). Each focal fish was transported inside this start box and placed individually in the central compartment of a new 189-L ( $89 \times 50 \times 50$  cm) aquarium. Fish in the start box were transported between tanks for Experiment 1 and Experiment 2 in a container of water ( $25 \times 17 \times 15$  cm) and were gently submerged into their new tank within this start box. The start box was placed so that the sliding door faced directly toward the camera, and away from each end chamber containing a stimulus. The central compartment (40 cm wide) of the test aquarium was separated by transparent partitions from two end chambers (each 23 cm wide; see Figure 1B). One end compartment con-

tained three conspecifics, while the opposite end compartment contained a single conspecific. The stimuli fish were always placed in the test tank 10 min before the focal fish. Stimuli fish (the conspecifics in end chambers) always came from a different stock than the focal fish and hence were all unfamiliar to the focal individual. Stimuli fish were always selected randomly and varied in terms of sizes and sexes and were changed across trials. The central chamber was further divided into three compartments labelled X, Y, and Z. Compartments X and Z (both 12.5 cm wide) were our “choice” zones, if the focal fish was in one of these zones it was considered to prefer one stimulus over the other. Compartment Y (17.5 cm wide) was labelled a “neutral” zone, where the focal fish was considered to have no preference. Each focal fish was given 5 min to acclimate in the start box before the sliding door was removed remotely. Once the door of the start box was opened, fish were then given a maximum of 5 min to leave. After the fish had left the start box or if the fish had not moved out of the start box after 5 min, the entire box was remotely removed from the tank. This removal forced fish to exit if they had not yet left the start box (forced exits occurred in 0 of 25 *N. pulcher* trials; 7 of 25 *T. temporalis* trials; 8 of 24 *N. multifasciatus* trials; 7 of 24 *A. compressiceps* trials; 6 of 24 *J. ornatus* trials; and 19 of 24 *N. tredocephalus* trials). From the moment the focal fish left the start box, they were recorded for another 20 min, moving around in the middle chamber and potentially interacting with conspecifics in both end chambers. Two predatory cichlids, *Lepidiolamprologus kendalli*, in mesh baskets were placed along the back wall of the central compartment to create a sense of predation risk and heighten the consequences of isolation.

### Quantification of Behaviour From the Videos

Preferences of focal fish were recorded with Canon cameras (HF S200 and HF R80) placed in front of each tank 1h prior to the start of each trial. Experiment 1 employed a forced choice design;

fish were always with one stimulus or the other and the focal fish was considered to be on a particular side (i.e., with a particular stimulus) if its head and gills were over the midway line. In Experiment 1, we recorded the time spent on each side of the tank (i.e., the time spent with each stimuli fish). Activity of stimuli fish was qualified by recording whether each fish was active or not every 2 min throughout the experiment. We got an activity rating every 2 min out of the 20 min trial, for a total of 10 observations. Experiment 2 allowed fish to have a no-choice option. If the focal fish was not in one of the “choice” zones near the conspecifics (either the group or the single conspecific), then it was considered to have no preference at that time. Again, the focal fish was considered to be in a particular zone if its head and gills were over the line to that zone. In Experiment 2, we recorded the time spent in each zone of the tank (zone “X” time near the single conspecific; zone “Y” no choice; and zone “Z” time near the group of conspecifics). We scored videos using Behavioural Observation Research Interactive Software (BORIS), a behavioural scoring program (Friard & Gamba, 2016). Videos were always scored by an observer who was blind to treatment. In Experiment 1, we started recording behaviours after the first 2 min to account for the disturbance caused by lifting the partitions. In Experiment 2, we recorded all behaviour for 20 min after the fish had left the start box.

### Statistical Analyses

Analyses were performed using R (v.3.6.0; R Core Team, 2019), and a significance ( $\alpha$ ) of 0.05 was used for all tests. When data failed to meet the assumptions of normality and homogeneity, the equivalent nonparametric tests were used. In Experiment 1 to assess whether a particular species is able to discriminate between familiar and unfamiliar conspecifics and if any corresponding preference was associated with social breeding system, we created a generalised least square (pGLS) model, which accounts for phylogenetic relationships between species, using the package “ape” (Paradis & Schliep, 2019). Branch lengths were estimated from the phylogeny presented by Day, Santini, and Garcia-Moreno (2007); however, assuming lambda ( $\lambda$ ) equals 1 produced the same result. We then used a Wilcoxon signed-ranks test to assess whether the familiarity preference for each species differed significantly from zero. We conducted 140 Day 3 trials (see online supplemental materials), but 19 of these trials (5 *N. pulcher*, 1 *T. temporalis*, 7 *N. multifasciatus*, 5 *A. compressiceps*, 1 *J. ornatus*), were eliminated and excluded from analyses because one of the fish jumped across the barriers during the trial or one fish did not move during the trial.

In Experiment 2, we investigated species differences for grouping using a Kruskal-Wallis one-way analysis of variance test. To compare time spent with the single conspecific versus time spent with the group, across all species combined, we used a Wilcoxon’s matched-pairs signed-rank test. Next, to assess each species’ individual preference (for the single conspecific or the group), we conducted a Wilcoxon’s matched-pairs signed-rank test on data for each species separately. Overall, our statistical analyses were based on six cichlid species and a total of 146 trials.

## Results

### Social Discrimination

On Day 2, there was no difference between cooperative and noncooperative cichlids in the time spent with the unfamiliar conspecifics (pGLS:  $\lambda = 0.18$ ,  $t_{(1,5)} = 0.41$ ,  $p = .71$ ). On Day 3, both cooperative and noncooperative cichlids showed consistent preferences for one of the conspecifics, suggesting that all six species are capable of social discrimination. However, the direction of that preference varied between cooperative and noncooperative species (see Figure 2), with cooperative species showing a preference for familiar fish (Wilcoxon’s-test,  $\mu = 0$ : *N. pulcher*,  $Z = 3.73$ ,  $p < .001$ ; *N. multifasciatus*,  $Z = 4.34$ ,  $p < .001$ ; *J. ornatus*,  $Z = 4.53$ ,  $p < 0.001$ ) and noncooperative species preferring the unknown or unfamiliar individuals (Wilcoxon’s-test,  $\mu = 0$ : *T. temporalis*,  $Z = 4.75$ ,  $p < .001$ ; *A. compressiceps*,  $Z = 3.75$ ,  $p < .001$ ; *N. tretocephalus*,  $Z = 4.61$ ,  $p < .001$ ). There were no differences in activity levels between the two stimulus fish (Wilcoxon’s test:  $Z = 0.38$ ,  $p = .35$ ).

### Quantity Discrimination

In this experiment, 5/6 species spent more time with the group of three fish versus the single fish. Although *N. multifasciatus* spent more time with the group than the single fish, this preference did not reach statistical significance (Wilcoxon’s test: *N. pulcher*,  $Z = 4.08$ ,  $p < .001$ ; *T. temporalis*,  $Z = 3.66$ ,  $p < .001$ ; *N. multifasciatus*,  $Z = 1.67$ ,  $p = .09$ ; *A. compressiceps*,  $Z = 4.41$ ,  $p < .001$ ; *J. ornatus*,  $Z = 4.56$ ,  $p < 0.001$ ; *N. tretocephalus*,  $Z = 2.53$ ,  $p = .012$ ; Figure 3). Males and females spent similar amounts of time with the group of three fish (Linear model [LM]:  $\chi^2_{(3, 145)} = 1.54$ ,  $p = .13$ ), and body mass of the focal fish did not influence the time spent with the group (LM:  $\chi^2_{(3, 145)} = 0.56$ ,  $p = .58$ ).

## Discussion

Familiarity plays a key role in social grouping decisions. For example, cattle (*Bos taurus*), red jungle fowl (*Gallus gallus*), and group-living predatory mites (*Phytoseiulus persimilis*) preferentially join familiar social groups (Muleta & Schausberger, 2013; Sato, Wood-Gush, & Wetherill, 1987; Väisänen & Jensen, 2004). Similar results have been shown in guppies (*Poecilia reticulata*), minnows (*Phoxinus phoxinus*), sticklebacks (*Gasterosteus aculeatus*), rainbowfish (*Melanotaenia* spp.), and cichlids (*Pelvicachromis taeniatus* and *Neolamprologus pulcher*; Barber & Wright, 2001; Brown, 2002; Frommen, Mehli, Brendler, & Bakker, 2007; Jordan, Wong, & Balshine, 2009; Lachlan, Crooks, & Laland, 1998; Thünken, Hesse, Bakker, & Baldauf, 2016). In the chub (*Leuciscus cephalus*), even familiar heterospecifics are preferred over unfamiliar conspecifics (Ward, Axford, & Krause, 2003). Preferentially shoaling with familiar individuals can lead to enhanced and more cooperative antipredator behaviour (as seen in fathead minnows, *Pimephales promelas*; Chivers, Brown, & Smith, 1995) and to more efficient prey location and consumption (as observed in three-spined sticklebacks, *Gasterosteus aculeatus*; Ward & Hart, 2005). Then why did the noncooperative cichlids prefer unfamiliar individuals while the cooperative and highly social cichlids preferred familiar individuals? More solitary ani-



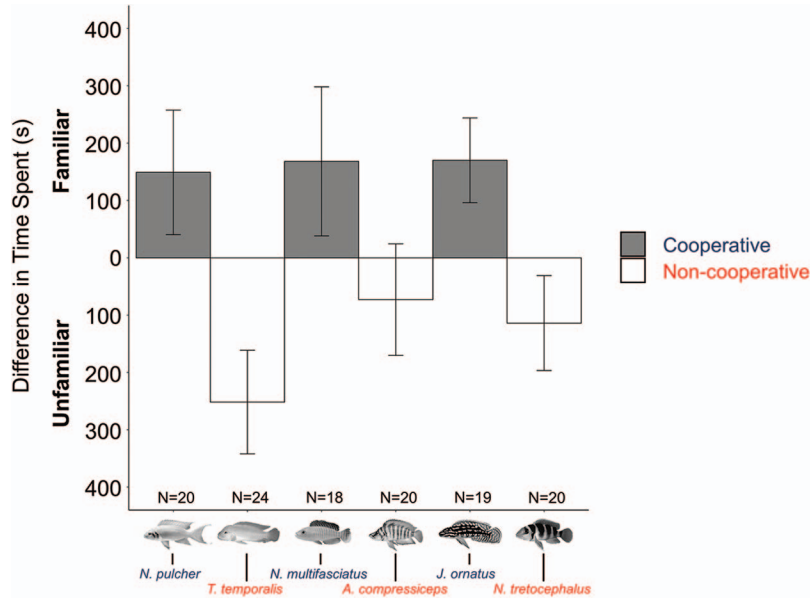


Figure 2. Familiarity preferences of cooperative and noncooperative cichlids. Social system predicted preference (pGLS:  $\lambda = 0.18$ ,  $t_{(1,5)} = 5.46$ ,  $p < .01$ ). Values are  $M \pm SEM$ . See the online article for the color version of this figure.

mals could use different tactics to solve conflicts, and interest in unfamiliar fish or objects may be driven by a more general preference for novelty (Brown, 2002; Hick et al., 2014). Novelty seeking offers opportunity for social interaction with unknown individuals and groups and increased sampling of the environment (Greenberg, 2003). In contrast, cooperative species’ familiarity preference may make sense, as the social landscape is stable, and familiarity facilitates altruism or reciprocity while dampening conflict in situations where interactions are regular. Familiarity allows

better predictions about how a companion will respond in a variety of contexts (Brown, 2002). In many territorial species, like the cichlids used in this study, territory owners act less aggressively to neighbours versus strangers, a phenomenon known as the “dear enemy” effect, which requires recognition of familiar individuals (Jaeger, 1981; Sogawa & Kohda, 2018; Temeles, 1994). Thus, territoriality may be a good proxy for social recognition capacity (Saeki, Sogawa, Hotta, & Kohda, 2018). In our study, the cooperative and noncooperative species showed consistent preferences

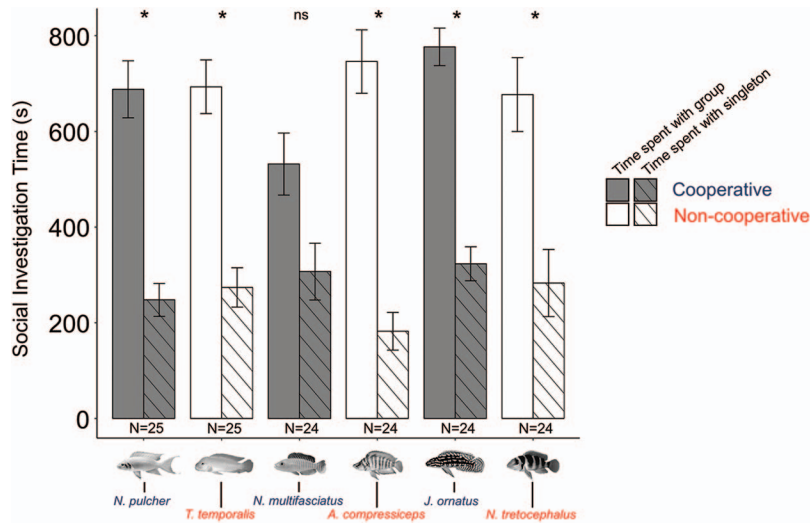


Figure 3. Grouping preferences of cooperative and noncooperative cichlids in the presence of predators. Overall, there was a strong preference for the group (Wilcoxon’s test:  $Z = 7.98$ ,  $p < .001$ ), and there were no differences between species in the strength of this preference (Kruskal-wallis [KW]:  $\chi^2_{(1,5)} = 7.92$ ,  $p = .16$ ). Values are  $M \pm SEM$ . \*  $p < 0.05$ . See the online article for the color version of this figure.

for familiar and unfamiliar individuals respectively, suggesting that all six species were able to differentiate between them, significantly expanding the known examples of social recognition in fishes (Experiment 1). Contrary to our prediction, both cooperative and noncooperative species demonstrated similar social recognition capacities and differential treatment of familiar versus unfamiliar individuals.

The ability to distinguish large from small or many from few can greatly impact an individual's fitness. Most fishes tested to date have shown preferences to join the larger of two shoals when provided an option (Agrillo & Dadda, 2007; Binoy & Thomas, 2004; Hoare, Couzin, Godin, & Krause, 2004; Krause & Godin, 1994; Pritchard, Lawrence, Butlin, & Krause, 2001). Larger groups offer a variety of fitness benefits such as protection from predators and the opportunity for social learning from more experienced individuals (Cresswell & Quinn, 2011; Laland & Williams, 1997; Mooring & Hart, 1992). In goldfish (*Carassius auratus*) and minnows (*Phoxinus phoxinus*), larger shoals find food faster (Pitcher, Magurran, & Winfield, 1982). Moreover, female sand gobies (*Pomatoschistus minutus*) choose males with more eggs in their nest, thereby using social information to inform mate-choice decisions (Forsgren, Karlsson, & Kvarnemo, 1996). Mosquitofish (*Gambusia affinis*) are even capable of discriminating between two shoals that differ in size by a single individual (Agrillo et al., 2008). In Experiment 2, cichlids were offered the choice between shoaling with a group of three or a single conspecific (accompanied by cues of predation risk), and 5/6 species spent more time with the group in this context. Although *N. multifasciatus* also spent more time with the group, this pattern did not reach statistical significance. The preference for the group in all cases reflects the direct benefits of grouping under threat of predation. We show that grouping is largely driven by threat of predation, irrespective of the social breeding system exhibited by a species and that both cooperative and noncooperative species have similar group-size assessment capabilities.

Overall, our results underscore the evolutionary forces that drive socio-cognitive abilities and suggest that ecological challenges, encountered by both cooperative and noncooperative animals, may play a greater role in shaping cognition than social challenges. Future experiments that manipulate familiarity in the context of shoal choice and quantity discrimination would shed light on the relative importance of these factors in group-joining decisions. Moreover, assessing the nature of the social interactions and comparing other socio-cognitive traits such as observational learning and collective decision making between cooperative and noncooperative animals would provide insight into whether there have been consistent cognitive changes in response to an assortment of social challenges.

## Résumé

La coopération est une interaction sociale très complexe qui nécessite souvent une coordination et une communication entre deux individus. La réciprocité s'explique en partie par la façon dont la coopération évolue et est entretenue; par exemple, le fait d'aider un individu sera éventuellement remis « en nature ». Pour que la réciprocité fonctionne, les individus doivent être en mesure de différencier ceux qui les ont précédemment aidés par opposition à ceux qui les ont « trompés ». Cependant, il existe peu de preuves

empiriques constatant de la capacité de reconnaissance accrue des espèces coopératives par rapport aux espèces non coopératives. Nous avons mené une étude comparative pour aborder cette question en observant trois cichlidés pratiquant la reproduction communautaire et trois de leurs proches parents qui ne pratiquent pas cette forme de reproduction, tous du lac Tanganyika. Lors de la première expérience, nous avons offert à un poisson le choix de passer du temps avec un congénère connu par opposition à un congénère inconnu, et avons constaté que les cichlidés coopératifs passent plus de temps avec les individus qu'ils connaissent, tandis que les cichlidés non coopératifs passent plus de temps avec des congénères inconnus. Dans le cadre d'une seconde expérience, nous avons donné le choix aux cichlidés de s'affilier à un ou à trois congénères (tous inconnus), et avons constaté que 2 cichlidés coopératifs sur 3, et que 3 cichlidés non coopératifs sur 3, préféreraient vivement s'affilier à de plus grands groupes. Nos résultats donnent à penser que tant les cichlidés coopératifs que les cichlidés non coopératifs ont développé la capacité à reconnaître les congénères connus, et qu'ils ont une préférence pour l'affiliation; cependant, la nature de ces préférences diffère d'une espèce à l'autre.

*Mots-clés* : cognition, discrimination, familiarité, reconnaissance, mémoire sociale.

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Received September 28, 2019

Accepted April 17, 2020 ■