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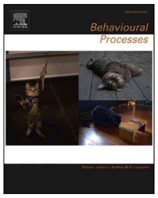

Rapid spatial learning in cooperative and non-cooperative cichlids

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ABSTRACT

The number, duration and depth of social relationships that an individual maintains can impact social cognition, but the connection between sociality and other aspects of cognition has hardly been explored. To date, the link between social living and intelligence has been mainly supported by studies on primates, and far fewer tests connecting sociality to cognitive abilities have used other taxa. Here, we present the first comparative study in fishes that examines whether complex social living is associated with better performance on a cognitively demanding spatial task. Using three cooperative, group-living cichlid fish species and three of their non-cooperative, more solitary close relatives, we studied maze learning and employed a new statistical extension for the 'lme4' and 'glmmTMB' packages in R that allows phylogeny to be included as a random effect term. Across trials, the three cooperative and the three non-cooperative species completed the maze faster, made fewer mistakes, and improved their inhibitory control. Although fish improved their performance, we did not detect any differences in the extent of improvement between cooperative and non-cooperative species. Both the cooperative species and the non-cooperative species took similar amounts of time to complete the maze, had comparable numbers of mistakes, and exhibited similar inhibitory control while in the maze. Our results suggest that living and breeding in complex social groups does not necessarily imply enhancement of other forms of cognition nor, more specifically, an enhanced spatial learning capacity.

1. Introduction

Many animals are "asocial" and live with or interact with other individuals for only a short period of their lives (e.g. while mating or caring for young), while others spend their entire lives with the same relatively stable group of individuals (Kutsukake, 2009; Ward and Webster, 2016). The *Social Intelligence Hypothesis* posits that animals living in conditions with greater social complexity have evolved enhanced cognitive abilities to cope with the difficulties of social life (Byrne, 1994; Byrne and Whiten, 1988; Holekamp, 2007). Some versions of the *Social Intelligence Hypothesis* suggest that social living favours social cognition specifically, while other versions argue that social living has a broader impact on cognition (Byrne and Whiten, 1988; Whiten and Byrne, 1997; Whiten, 2000). Much work has been done to investigate the relationship between social complexity and brain size evolution; however, the critical cognitive mechanisms that co-evolved with group-living and enable a highly social lifestyle have not received the same attention (Ashton et al., 2018; Johnson-Ulrich, 2017; Kummer et al., 1997; Reader and Laland, 2002).

The most tightly knit and well-coordinated group-living species are cooperatively breeding animals. In cooperatively breeding social groups, subordinate group members aid dominant group members in the care of the dominant's young (Solomon and French, 1997). Researchers have argued that cooperative breeding requires that individuals recognize their own group-members, remember past interactions, and use this information to inform future behaviour (Iwaniuk and Arnold, 2004; Reddon et al., 2016; Thornton and McAuliffe, 2015). Hence, social memory and cheater detection (the ability to discern whether group-members are performing tasks that benefit the group) are thought to be important cognitive traits in the evolution of cooperation (Burkart and van Schaik, 2010; Dugatkin, 2002; West et al., 2007). Cooperative breeding also requires the formation of strong and stable social bonds and the ability to resolve conflict within a group (Balshine et al., 2017; Hick et al., 2014; Reddon et al., 2019). A hypothesis known as the *Cooperative Breeding Hypothesis* suggests that social challenges are especially pronounced in cooperatively breeding groups, as these animals often live in strict hierarchies for which they must remember their relative rank, and monitor the rank and contributions of others (Burkart

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and van Schaik, 2010; Iwaniuk and Arnold, 2004; Thornton and McAuliffe, 2015). Thus, according to this second hypothesis, cooperative breeders are expected to have highly developed socio-cognitive abilities (Burkart and van Schaik, 2016). Our aim was to investigate whether the enhanced socio-cognitive ability expected to develop in highly social species according to the *Cooperative Breeding Hypothesis*, might also extend to other domains, giving these highly social species an advantage when performing other cognitive tasks.

Spatial navigation is one such cognitive task and is a key requirement for foraging, migration and predator avoidance; activities that are directly linked to fitness and can have a social component (e.g. local enhancement in foraging; Burns and Rodd, 2008; Fagan et al., 2013; Fukumori et al., 2010; Pravosudov and Roth, 2013). The degree of habitat complexity that an animal needs to contend with is known to shape the brain (Carbia and Brown, 2019). In small mammals, like North American sciurids (e.g. squirrels), arboreality is the best predictor of relative brain size and is highly correlated with habitat (Budeau and Verts, 1986). In fishes, examples linking brain and habitat come from cichlid fishes, where species inhabiting structurally complex underwater environments often have larger telencephalons (Ectodini clade; Pollen et al., 2007), and the same has been shown for sunfish (*Lepomis gibbosus*; Axelrod et al., 2018), and sticklebacks (*Pungitius pungitius*; Gonda et al., 2009). The telencephalon is part of the teleost forebrain, and hosts the lateral telencephalic pallium, an area thought to represent the fish homologue of a hippocampus—the brain structure implicated in spatial learning and memory of mammals and birds (Durán et al., 2010; Rodrıguez et al., 2002; Vargas et al., 2009). Studies that lesion or ablate part of the telencephalon in fishes confirm its prominent role in spatial learning (Broglio et al., 2003; Riedel, 1998), but the telencephalon is also involved in the regulation and expression of social behaviour (Flood and Overmier, 1981; Scace et al., 2006). Although the role of habitat complexity in sculpting the fish brain is well established (Gonda et al., 2009; Kotrschal and Taborsky, 2010; Salvanes et al., 2013; Strand et al., 2010; White and Brown, 2015), little is known about how the demands of complex group-living (i.e. social complexity) might shape the fish brain. Also, cognitive differences or advantages might not manifest as visible changes in brain morphology or brain size, which makes understanding the connection between social complexity, and other cognitive abilities like spatial cognition, particularly difficult.

Sex also impacts the brain through differential expression of key hormones such as testosterone and estrogen, which have implications for things like motivation (Becker and Taylor, 2008) and metabolism (Hewitt et al., 2003), and consequently behaviour and/or cognition. In humans, for example, males often outperform females on dynamic 3-dimensional spatial tasks and these sex differences are attributable to proximate biological mechanisms (e.g. sex hormones) and developmental mechanisms (e.g. play patterns; Geary, 1995). Recent research suggests that differences in wayfinding and navigational strategies in humans are further influenced by environment and experience (Livingstone-Lee et al., 2014), and that females are better able to use mapping strategies (allocentric methods i.e. remembering elements in the environment, allowing the formation of real-world representations) in order to effectively navigate their environment. That said, multiple strategies are used in tandem and are frequently switched, integrated, and combined (Fernandez-Baizan et al., 2019). In fishes, a number of previous studies have found sex differences in performance during spatial challenges (in the guppy *Poecilia reticulata*, Reader and Laland, 2000, in the cichlid *Astatotilapia burtoni*, Wallace and Hofmann, 2021, as well as other fish species, Costa et al., 2011). However, sex differences in non-spatial tasks are seldom observed (e.g. discrimination of food quantities, object recognition memory; Lucon-Xiccato and Bisazza, 2017a; 2017b). Similar to humans, sex differences in the use of navigational strategies have also been described in a number of fish species (Salena et al., 2021). As such, we might expect to find sex-specific differences in spatial abilities for other fishes.

Here, we describe a comparative study that assessed whether spatial learning and memory performance differed between three cooperatively breeding cichlid fish species and three of their non-cooperative relatives, and further investigated for sex differences. All six species were Lamprologini cichlids, a tribe of fish from Lake Tanganyika in Africa (Day et al., 2007) and a clade that has evolved group-living and cooperative breeding on five separate occasions (Dey et al., 2017; Reddon et al., 2017). While many Lamprologini species live in social groups, rely on conspecific group members for protection and cooperate to raise young, other closely related Lamprologini species rarely interact with conspecifics (apart from their mated partners or with a neighbour during a territorial standoff). These less social species do not cooperate, nor do they form permanent groups (Balshine et al., 2017; Hick et al., 2014). Using a maze learning paradigm with repeated trials to assess spatial learning and memory, we tested the following six territorial Lamprologini cichlids: the three cooperatively breeding cichlid species were *Neolamprologus pulcher*, *Neolamprologus multifasciatus* and *Julidochromis ornatus*, and the three non-cooperative species were *Telmatochromis temporalis*, *Altolamprologus compressiceps* and *Neolamprologus tretocephalus* (see Supplementary Fig. 1 for additional details on the evolutionary relations of these species and the morphological measures of the individuals used). These fishes have fairly comparable habitats, and can all be found in shallow rocky areas of Lake Tanganyika (Barlow, 2008; Brichard, 1989; Konings, 1998). Hence, these closely related but socially diverse species offer a powerful model system to explore how social living molds the brain and cognitive abilities.

We hypothesized that the cooperative species would initially outperform the non-cooperative species, and improve more or get faster over repeated trials. We reasoned that because cooperatively breeding species must cope with the cognitive demands of social life, this lifestyle might make them better problem solvers in other aspects of cognition, and lead to enhanced spatial performance in the maze. Furthermore, because animals that live in groups often subdivide their territories to avoid conflict over space-use (Effenberger and Mouton, 2007; Schradin and Lamprecht, 2002; Werner et al., 2003), we posited that group-living and cooperatively breeding species may require a more detailed delineation of their territorial space—to adhere to their individual sub-territories. Thus, we expected that this would lead to better spatial performance in the cooperative species. Additionally, in many cichlids including *N. pulcher*, males have larger home ranges and disperse sooner and faster than females (Stiver et al., 2007; Desjardins et al., 2008; Wong et al., 2012) and we therefore predicted that males across all six species would complete the maze faster than females.

2. Methods

2.1. Animals and housing conditions

All fish were housed in the Aquatic Behavioural Ecology Laboratory at McMaster University, Hamilton, Ontario, Canada. Morphological information regarding our study specimens can be found in the supplementary material (see Supplementary Tables 1 and 2). *N. pulcher* and *T. temporalis* were the descendants of wild caught fishes from Lake Tanganyika, Africa, while *N. multifasciatus*, *A. compressiceps*, *J. ornatus* and *N. tretocephalus* were purchased from a commercial aquarist supplier (Finatics, Mississauga, Ontario, Canada). Prior to the experiment, fishes were held in mixed-sex stock tanks equipped with filters, heaters, coral sand substrate, terracotta flowerpot halves and opaque PVC tubes (10 cm in diameter and 25 cm in length) provided as shelter. *N. pulcher*, *T. temporalis*, *A. compressiceps*, and *J. ornatus* were held in 568 L tanks containing approximately 40 individuals per tank and *N. multifasciatus* and *N. tretocephalus* were held in 189 L tanks with approximately 20 individuals per tank. These stock tanks and our experimental tank with the maze (see below) were all maintained at 25–28°C and under a 12L:12D photoperiod. Fish were fed a diet of flakes and floating pellets six times per week, with occasional supplementation of brine shrimp.

2.2. *Spatial learning trials*

In preparation for the experiment, each focal fish was captured from that species' respective stock tank by being gently guided with a hand net into a start box. The start box was a black PVC tube closed off permanently at one end, with a sliding door attached to a pulley at the other end. The focal fish in the start box was always placed at one end of the maze, in the start zone (Fig. 1a). Three conspecifics from a different mixed sex stock tank (and therefore unknown to the focal individual) were also captured at random and placed in a perforated transparent PVC cylinder (11 cm in diameter and 32 cm in length) at the opposite end of the maze, in the completion zone. The random selection of stimulus fish meant that the sex ratios of these groups were not controlled and hence differed among focal fish, and species. The transparent PVC tube and its perforations allowed for the exchange of water between the cylinder containing conspecifics and the aquarium, and for visual, olfactory and acoustic cues to pass between the focal and stimulus fish. The fish were run repeatedly through the maze, which had a similar layout to mazes used in other studies (Girvan and Braithwaite, 1998; Lucon-Xiccato and Bisazza, 2017b), and which sat inside a 189 L (89 × 50 x 50 cm) aquarium. The maze was constructed using both opaque and transparent PVC and contained a series of transparent PVC barriers (5 cm wide) running down in the middle section of the maze. These transparent barriers down the middle allowed the focal fish to view the mixed sex stimulus group (in the completion zone) in each section of the maze. The maze also had opaque PVC barriers and one correct open route that led to the completion zone (Fig. 1b) as well as blind alleys and false openings or dead-ends. When fish entered these dead-end corridors, they were considered to have made a wrong turn or a mistake. The maze had four compartments: a start zone, two intermediate zones (zones 1 and 2), and a completion zone. Each of these zones were identical in size (16 cm in length).

After being placed in the start zone, each focal fish was given 1 h to recover from capture and transport, and to acclimate in the start box before the sliding front door was removed remotely. After the door had been removed, fish were then given a maximum of 5-minutes to leave the start box. If the fish had not left the start box after 5-minutes, the box was remotely lifted out of the tank from the back, and the fish were tipped out and forced to leave the start box. Once the focal fish left the start box, on its own volition or by being forced to exit when the box was removed, each fish then had a maximum of 2-hours to navigate the maze and reach the completion zone containing the group of conspecifics. Forced exits occurred in 2/15 *N. pulcher* trials, 2/11 *T. temporalis* trials, 12/23 *N. multifasciatus* trials, 7/18 *A. compressiceps* trials, 3/12 *J. ornatus* trials and 14/16 *N. tretocephalus* trials. Upon reaching the completion zone, re-entry into the maze was blocked off with an opaque barrier. The maze apparatus was then lifted and reversed in the tank, so that for the next trial, the maze was oriented in the opposite direction to how it had been on the previous trial. By reversing the maze apparatus, the focal fish could traverse the maze in the opposite direction while still experiencing the same layout as it had on the previous trial without requiring that it return to the original start zone. The cylinder containing the stimulus fish was lifted and placed at the opposite end (the previous start zone was now the new completion zone for the next trial). If after 2-hours (the trial maximum time) the fish had not yet completed the maze, the fish was gently guided to the completion zone using a hand net, and a barrier was placed so that the maze direction could be reversed and the cylinder side could be switched as described above, while the fish was occluded. The maze water was mixed between trials. Also, between trials 1–2 and 2–3, the focal fish was given 30-minutes to acclimate in its new start zone before the barrier was lifted and the fish were once again able to access the maze. Each focal fish had the opportunity to explore the maze three times in total.

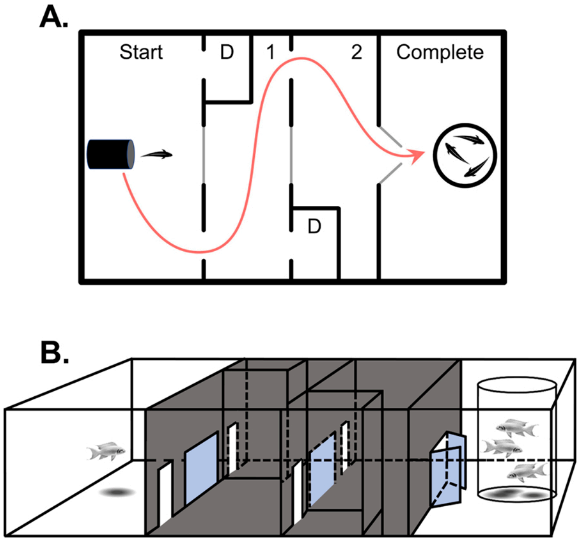

Fig. 1. a. Schematic of the experimental aquarium (bird's eye view) used for the maze learning experiment. The *black lines* represent opaque barriers and the *gray lines* represent transparent barriers. The 'Start' marks the starting zone and the 'Complete' marks the completion zone. The '1' marks zone 1 and the '2' marks zone 2. The 'D' represents dead-end corridors. To access the completion zone, the fish would need to navigate along the path illustrated in red. **b.** Schematic of the experimental aquarium (eye level view). The blue panels represent transparent barriers through which the focal fish could see the stimulus group, and the gray panels represent opaque barriers. The white panels represent openings through which the fish could swim to access a dead-end corridor or the route through the maze.

2.3. *Quantification of behaviour*

Trials were video recorded from above with a Canon HF R80 camera. The camcorder was controlled remotely, and the experimenter was able to monitor the progress of the focal fish after they had left the room. We scored the videos using BORIS, a behavioural observation scoring software (Friard and Gamba, 2016) and recorded the latency to leave the start box, as well as the time until the focal fish reached zones 1 and 2 and the completion zone. We also noted the number of times that each fish entered a dead-end corridor and classified each entry as a mistake. Finally, as a measure of inhibitory control, we recorded the number of times that each fish would swim directly into the transparent barriers that ran down the middle of the maze, where each distinguishable forward movement made towards the barrier was counted and tallied. The term inhibitory control describes an individual's ability to resist an urge or inhibit a behavioural propensity to obtain a reward, and is an increasingly common measure of cognitive ability (Brandão et al., 2019; Bray et al., 2014) that has recently gained traction in fish studies (Brandão et al., 2019; Gatto et al., 2018; Lucon-Xiccato et al., 2017). For each trial, we recorded and continually monitored location until the focal fish reached the completion zone or when a maximum of 2-hours had elapsed.

2.4. *Statistical analysis*

Because individuals that did not complete the maze all three times did not have the same learning opportunities or experiences as those that completed the maze three times, data from these individuals without three runs were removed in the analyses (0/15 *N. pulcher*, 9/23 *N. multifasciatus*, 3/12 *J. ornatus*, 3/11 *T. temporalis*, 2/18 *A. compressiceps*, and 14/16 *N. tretocephalus*). However, when all of the data and individuals were included in the analyses (including individuals who only completed the maze once, twice or three times), the results were similar and these more inclusive but less conservative results can be viewed and are discussed in the supplementary material (see Supplementary Fig. 4).

To analyze the relationship between time to maze completion and each of our predictor variables (social system, sex and trial number) we fitted linear mixed models (LMMs) using the “lme4” package (Bates et al., 2015). The time to completion data were log transformed prior to analyses to meet the assumptions of normality and homoskedasticity. We included each of our predictor variables and their interaction terms as fixed factors. Species and individual fish ID were also included as random effects in each model, because we were not directly interested in whether there was a difference among species, or individuals, but wanted to provide some control for these variables. The random effect of species was used as a phylogenetic control, but the true phylogenetically controlled models are reported and discussed fully in the supplementary materials. We constructed GLMMs (negative binomial family) to assess whether there were differences between cooperative and non-cooperative species, and between the sexes, in the number of mistakes (i.e. dead-end corridor entry) and the degree of inhibitory control (i.e. the number of times that a fish swam directly at transparent barriers). All models used the same fixed and random effects. In order to assess whether the rates of improvement across trials differed between cooperative and non-cooperative species, and males and females, we analyzed the two-way interactions between social system and trial, and sex and trial. Assumptions for the linear mixed models were visually assessed using quantile-quantile and scale-location plots, while the assumptions for the generalized linear mixed models were assessed by plotting the simulated residuals with the “DHARMa” package. The effects of each model were evaluated using the Anova function from the “car” package.

Phylogenetically controlled linear mixed models and phylogenetically controlled generalized linear mixed models were also constructed using methods described by Li and Bolker (2019). These methods manipulate the ‘lme4’ and ‘glmmTMB’ packages to include phylogenetic signal as a random effect term. Importantly, these new methods are currently limited in their capacity to evaluate changes between trials, have not yet been used widely, and the patterns of results for these phylogenetically controlled models were not different from the models used here without phylogenetic control. We therefore only report the phylogenetically controlled analyses in the supplementary materials (see ‘Phylogenetically controlled models’ section in Supplementary Materials). Note that the phylogenetically controlled models presented in the supplementary materials include analyses for *all* data and *all* individuals, regardless of whether they only completed the maze once, twice, or three times and the evaluation of these data are the focus of the supplementary portion of this paper. In the following section, the analyses were conducted using data from 65 fishes and 195 trials. Analyses were performed with R (v.3.6.3, R Core Team, 2020) and a significance level (α) of 0.05 was used for all tests.

3. Results

3.1. Social system

The three cooperative species did not complete the maze any faster than the three non-cooperative species (Fig. 2a; log-LMM: $\chi^2 = 2.07$, df $= 1$, $p = 0.15$). Both cooperative and non-cooperative species completed the maze faster across trials (log-LMM: $\chi^2 = 30.70$, df $= 2$, $p < 0.001$; Supplementary Fig. 2a cooperative, 2d non-cooperative), and there was no significant difference in their rates of improvement i.e. in the reduction in time taken to complete the maze across trials (Social System*Trial Number, log-LMM: $\chi^2 = 0.57$, df $= 2$, $p = 0.75$). Cooperative and non-cooperative species made similar numbers of mistakes or dead-end corridor entries (GLMM: $\chi^2 = 1.47$, df $= 1$, $p = 0.23$; Fig. 2b) and both types of species made fewer mistakes over repeated trials (GLMM:

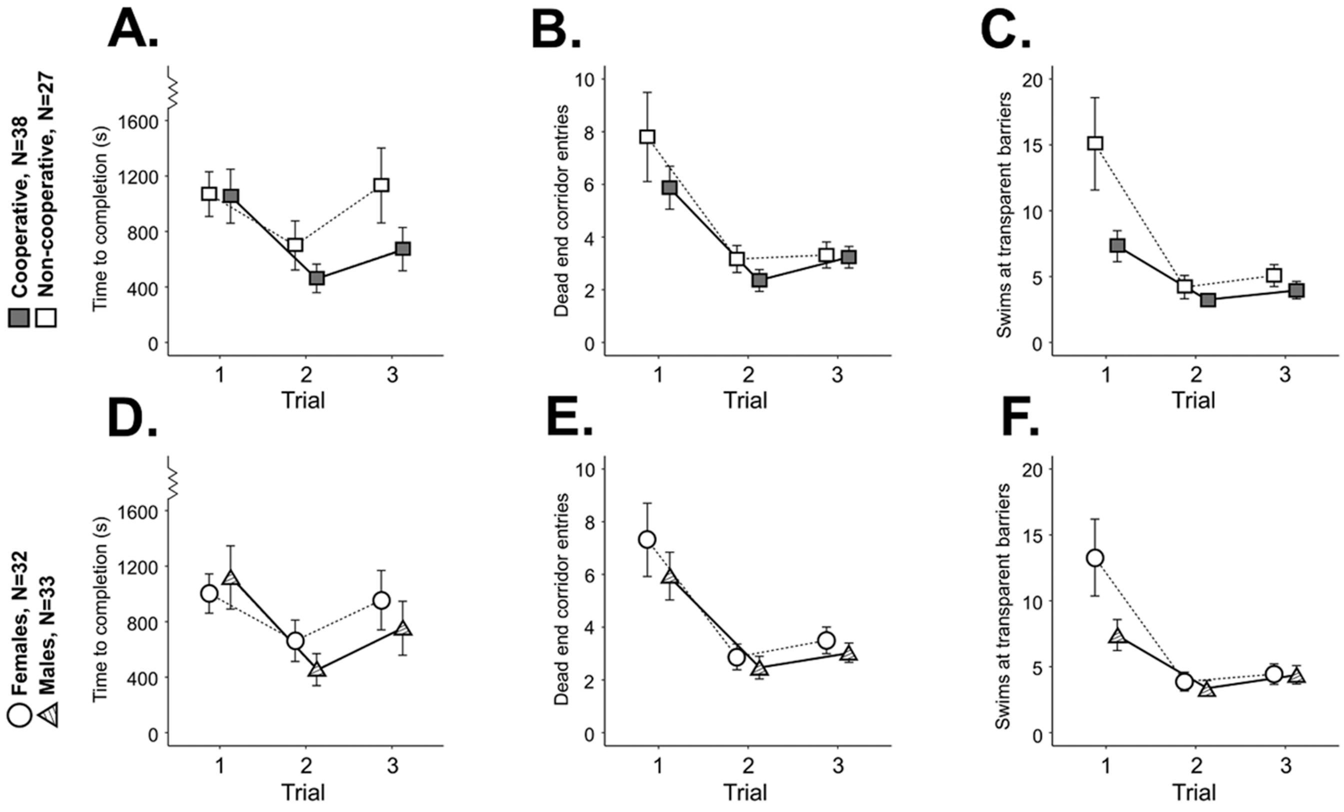

Fig. 2. a/d. The time (in seconds) taken to complete trials 1–3 (2a social system; 2d sex). **b/e.** The number of dead-end corridor entries (2b social system; 2e sex). **c/f.** The number of attempts to get through the transparent barriers/inhibitory control (2c social system; 2f sex). All data removed for individuals that did not complete the maze on any of the three trials. Values are means ± SEM.

$\chi^2 = 35.87$, df $= 2$, $p < 0.001$; Supplementary Fig. 2b cooperative, 2e non-cooperative). There was no significant difference in the rate of improvement in terms of mistakes made between cooperative and non-cooperative species (Social System*Trial Number, GLMM: $\chi^2 = 0.72$, df $= 2$, $p = 0.70$). Generally, we observed variable and individualized responses by the fish that entered the dead-ends; some individuals would enter and exit quickly, while others stayed in these areas and treated them as a shelter of sorts. Cooperative and non-cooperative species swam at the transparent barriers a comparable number of times (GLMM: $\chi^2 = 0.21$, df $= 1$, $p = 0.65$; Fig. 2c). Cooperative and non-cooperative species both swam at the transparent barriers fewer times across trials (GLMM: $\chi^2 = 50.74$, df $= 2$, $p < 0.001$; Supplementary Fig. 2c cooperative, 2f non-cooperative), and there was no significant difference for rates of improvement in relation to sociality (Social System*Trial Number, GLMM: $\chi^2 = 2.40$, df $= 2$, $p = 0.30$).

3.2. *Sex*

Males and females did not differ in the time taken to complete the maze (log-LMM: $\chi^2 = 0.42$, df $= 1$, $p = 0.52$; Fig. 2d). Across trials, both sexes completed the maze faster (log-LMM: $\chi^2 = 30.70$, df $= 2$, $p < 0.001$; Supplementary Fig. 3a males, 3d females), and males and females had similar rates of improvement in terms of the time taken to complete the maze (Sex*Trial Number, log-LMM: $\chi^2 = 2.29$, df $= 2$, $p = 0.32$). Males and females also made a similar number of mistakes and entered the dead-end corridors at a comparable frequency (GLMM: $\chi^2 = 0.67$, df $= 1$, $p = 0.42$; Fig. 2e). Both males and females made fewer mistakes across trials (GLMM: $\chi^2 = 35.87$, df $= 2$, $p < 0.001$; Supplementary Fig. 3b males, 3e females), and there was no sex difference in the rates of improvement (Sex*Trial Number, GLMM: $\chi^2 = 0.10$, df $= 2$, $p = 0.95$). Males and females did not differ in the number of times that they swam at the transparent barriers (GLMM: $\chi^2 = 0.14$, df $= 1$, $p = 0.71$; Fig. 2f), both improved and swam at the transparent barriers fewer times across trials (GLMM: $\chi^2 = 50.74$, df $= 2$, $p < 0.001$; Supplementary Fig. 3c males, 3f females), and there was no significant difference in their rates of improvement (Sex*Trial Number, GLMM: $\chi^2 = 1.62$, df $= 2$, $p = 0.44$). We did not observe any other significant effects or interactions.

3.3. *Supplementary exploratory analyses*

The results above included only individuals that completed the maze three times (see methods). However, the patterns of these results were largely unchanged when we included all collected data from *all* individuals and *all* trials (see Supplementary Figs. 4–6). The one exception was the time to completion of the maze, where including all data revealed a significant interaction between social system and trial number. In other words, when all data were analyzed together, cooperative species improved their time to completion over repeated trials more so than non-cooperative species, and this was also true for the models with phylogenetic control (see Supplementary Fig. 4a). In addition, because two species had low levels of participation (*N. tretocephalus* representing just a few participants, and *J. ornatus* with few female participants), we conducted exploratory analyses without these two species. While the patterns of the results were robust to the removal of the *J. ornatus*, when *N. tretocephalus* was excluded, we no longer detected any interaction between social system and trial number, suggesting the *N. tretocephalus* drove this one result. These analyses and the results for each individual species separately are all included in the supplementary materials linked to this paper (see Supplementary Figs. 7–12).

4. Discussion

Contrary to our predictions, we did not find compelling evidence that cooperative species outperformed their non-cooperative relatives in the spatial task. Both cooperative and non-cooperative cichlids took less time to complete the maze following the first trial. Cooperative species did not display better inhibitory control, nor did they make fewer mistakes than their non-cooperative relatives. Overall, our results suggest that the challenges of group-living and cooperation do not offer any advantages to spatial learning and memory in these fishes—cooperative and non-cooperative species performed comparably in all three spatial performance metrics and improved similarly in terms of these metrics.

Living in a social environment, forming and maintaining relationships, and working together to achieve shared goals are cognitively demanding challenges. However, what constitutes a social challenge and which challenges in particular are most influential as selective agents on brain evolution and cognition is unclear. In primates and ungulates, brain size is thought to be linked to group size (Dunbar and Shultz, 2007a; 2007b but see DeCasien et al., 2017, Lindenfors et al., 2021 and Powell et al., 2017 for an opposing view). In contrast, flock size in birds does not correlate with brain size, likely because large flocks can include thousands of birds and does not necessitate strong social bonds, and the same can be said for many mammalian species that live in large herds (van Horik and Emery, 2011). In some insects, like paper wasps (Vespidae family), colony size is in fact negatively related to brain size; wasp species that form larger groups have smaller brains because they can rely on their siblings or nestmates for information and division of labour, rather than produce information or perform certain tasks themselves (O'Donnell et al., 2015). Evidently, group size alone is an inadequate measure of social complexity, but researchers have not yet agreed on a suitable alternative (Kappeler, 2019).

Rather than group size, it may be the depth and longevity of social interactions that have a more profound influence on the brain (van Horik and Emery, 2011). Also, intricate social relations are not exclusive to group-living animals. Territorial animals, for example, are likely to have regular and prolonged interactions with mates, or with neighbouring territory owners, as well as other potential usurpers. All six of the cichlid species used in this study face similar challenges of having to find food and a mate, maintaining a pair bond, providing parental care, and acquiring, defending and maintaining a territory (reviewed by Sefc, 2011). It may be that it was these shared ecological and social challenges, and not the challenges posed by cooperative group living, that played a more prominent role in molding the cognitive abilities of these cichlids, including spatial cognition. Supportive of this idea, previous research comparing the brains of cooperative and non-cooperative Lamprologines has found no significant differences in whole brain masses (Reddon et al., 2016). Yet, notable research on cichlids of the Ectodini clade (also from Lake Tanganyika) suggests that regional brain size differences are pervasive and dependent on social factors (mating system), warranting future research into evaluating which particular social challenges are most important in shaping the brain as a whole and its various regions and structures (Pollen et al., 2007).

Despite our expectation for finding sex differences, we did not detect any major differences in maze performance between males and females. Sex differences in the brain are well documented in a wide variety of taxa, including fishes (Rhodes and Rubin, 1999; Goodson and Bass, 2001). While there are many striking similarities between the fish brain and the brains of other animals (Bshary et al., 2014), there are also some fundamental differences in neural architecture and organization which mean that the sex differences in cognitive ability reported in other animals might not be as apparent in some fishes (Ebbesson and Braithwaite, 2012). It is thought that the dominant role of hormones in the developing fish brain is activational, not organizational like in mammals and birds, so sex differences may be less prominent (Zakon, 2000). We might expect cognitive differences between male and female fish if each sex faces unique and different challenges (e.g. if the sexes eat different diets, or occupy different niches; Lucon-Xiccato and Bisazza, 2017a; Magurran and Garcia, 2000). This is likely the case for the many studies reporting sex differences in fishes (Costa et al., 2011; Lucon-Xiccato and Bisazza, 2017b; Roy and Bhat, 2018). The fish brain is also highly susceptible to changes based on experiential factors such as those presented by the physical and social environments (Ebbesson and Braithwaite, 2012) resulting in remarkable plasticity, and plastic responses that are often sex dependent (Kotrschal et al., 2012). For the cichlid species used in this study, both sexes experience many of the same ecological and social challenges. The comparable navigational scores for males and females reported here do not provide support for the notion of sex-specific spatial abilities in this group of fishes. Our findings may be explained by the overlap in challenges experienced by male and female pair bonded cichlids, and the limited action of gonadal steroids in organizing neural tissue in the fish brain (Sefc, 2011; Zakon, 2000). We suggest that sex differences in locomotion and dispersal previously reported in *N. pulcher* (Stiver et al., 2006; Stiver et al., 2007), might reflect differences in the spatial distribution of social opportunities available to each sex, or in the motivation to move, rather than differences in spatial capacity.

Future research could improve upon our study in a number of ways. First it would be valuable to retest using wild caught, rather than captive bred fishes (Christie et al., 2012; Doyle and Talbot, 1986; Huntingford, 2004; Huntingford et al., 1994; Salena et al., 2021). Second, between each trial we removed, reversed and replaced the maze in a different orientation to avoid having to capture, handle and stress the focal individual. However, in tasking the fish to go through the maze repeatedly and in opposite directions, the extra-maze cues (outside the tank e.g. lights, distance to walls) were altered between trials. In the future, the fish should be able to run through the maze with all external cues held constant. Third, the motivation to reach the social stimulus at the completion zone of the maze may have changed with each subsequent trial. We chose to use a social reward because in many studies animals prefer to join larger groups (Ashley et al., 1993; Hager and Helfman, 1991; Keenleyside, 1955; Krause and Godin, 1994; Svensson et al., 2000), and previous research on these particular Lamprologini cichlid species suggests that Lamprologines prefer to join large groups when threatened, regardless of their social breeding system (O'Connor et al., 2015; Salena and Balshine, 2020). The focal fish in our study were captured from their housing tank, placed in a start box and inserted into an unfamiliar tank before the first trial. In contrast, between trials two and three, in order to reduce stress, the fish were not captured; although if the fish did not complete the maze in the 2-hour trial period, they were gently guided to the completion zone using a hand net so that the next trial could be set-up while the focal fish was occluded behind an opaque barrier. Therefore, the perception of threat over subsequent trials was reduced and this may have changed the underlying motivation to join a group at the end of the maze under increasingly non-threatening conditions. Habituation to the maze also may have played a role. Fourth, we acknowledge that the social reward may have been more attractive to the cooperative species. However, given that the highly social species were not better at learning, this factor did not seem to confound our results. We only used conspecifics as stimuli after piloting other non-social rewards (food and shelter), but these did not have the same salience for focal fishes in our pilot studies. Additional exploration of how social motivation differs across species would be another valuable topic for future research (Balshine et al., 2017). Fifth, we had a relatively small number of species (N = 6) and also a small number of individuals were analyzed for some species because not all animals completed the maze three times. While it was beyond the scope of this study to evaluate the spatial performance in more than six species, including additional species, and additional individuals per species would be a valuable goal for future studies. And lastly, our study specimens demonstrated substantial improvement in only 3 trials, yet future studies that aim to assess spatial learning in these cichlids over a longer time frame may also benefit from making the task more difficult.

Although the cognitive challenges of social life may favour relatively larger neocortices in primates (Dunbar and Shultz, 2007a; 2007b), it is unclear how these same challenges affect the brains of other highly social animals (Iwaniuk and Arnold, 2004; Reddon et al., 2016), and which social challenges in particular are most influential in shaping the brain and cognitive abilities. In our experiment, we did not find compelling evidence for differing spatial performance between cooperative and non-cooperative species, or males and females. We did, however, find that both cooperative and non-cooperative species, and males and females, took less time to complete the maze over repeated trials, made fewer mistakes and improved their inhibitory control, which suggests that the animals learned and remembered the correct route. Our results do not provide support for enhanced cognition in cooperatively breeding animals for cognitive functions related to spatial navigation. We did not find evidence for a connection between sociality and performance on the spatial task, which indicates that performance in this particular task may not be linked to social factors. It remains possible that selection due to high degrees of sociality may act specifically on cognitive functions related to social behaviour (e.g. social memory, social learning). Taken together, our findings contribute to the growing body of literature surrounding the *Cooperative Breeding Hypothesis* (Thornton and McAuliffe, 2015) and ascertain that an accurate assessment of social complexity requires the consideration of multiple social variables.

Ethical note

All protocols were approved by the Animal Research Ethics Boards of McMaster University (Animal Utilization Protocol No. 18–04–16) and complied with the guidelines established by the Canadian Council on Animal Care (CCAC) regarding the use of animals in research and teaching.

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CRediT authorship contribution statement

Matthew G. Salena: Conceptualization, Methodology, Formal analysis, Investigation Writing – original draft, Writing – review & editing, Visualization. **Angad Singh:** Methodology, Investigation, Writing – review & editing. **Olivia Weller:** Investigation, Writing – review & editing. **Xiang Xiang Fang:** Investigation, Writing – review & editing. **Sigal Balshine:** Conceptualization, Methodology, Writing – review & editing, Supervision, Funding acquisition.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.beproc.2021.104550.

References

Ashley, E.J., Kats, L.B., Wolfe, J.W., 1993. Balancing trade-offs between risk and changing shoal size in northern red-belly dace (*Phoxinus eos*). Copeia 1993, 540–542. https://doi.org/10.2307/1447157.

Ashton, B.J., Thornton, A., Ridley, A.R., 2018. An intraspecific appraisal of the social intelligence hypothesis. Philosophical Transactions of the Royal Society B: Biological Sciences 373, 20170288. https://doi.org/10.1098/rstb.2017.0288.

Axelrod, C.J., Laberge, F., Robinson, B.W., 2018. Intraspecific brain size variation between coexisting sunfish ecotypes. Proceedings of the Royal Society B 285, 20181971. https://doi.org/10.1098/rspb.2018.1971.

Balshine, S., Wong, M.Y., Reddon, A.R., 2017. Social motivation and conflict resolution tactics as potential building blocks of sociality in cichlid fishes. Behavioural Processes 141, 152–160. https://doi.org/10.1016/j.beproc.2017.01.001.

Barlow, G., 2008. The cichlid fishes: nature's grand experiment in evolution. Basic Books,, New York.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Becker, J.B., Taylor, J.R., 2008. Sex differences in motivation. In: Becker, J.B., Berkley, K.J., Geary, N., Hampson, E., Herman, J.P., Young, E. (Eds.), Sex Differences in the Brain: From Genes to Behaviour. Oxford University Press, United Kingdom, pp. 177–199.

Brandão, M.L., de Almeida Fernandes, A.M.T., Gonçalves-de-Freitas, E., 2019. Male and female cichlid fish show cognitive inhibitory control ability. Scientific Reports 9, 1–8. https://doi.org/10.1038/s41598-019-52384-2.

Bray E., E., MacLean, E.L., Hare, B.A., 2014. Context specificity of inhibitory control in dogs. Animal Cognition 17, 15–31. https://doi.org/10.1007/s10071-013-0633-z.

Brichard, P., 1989. Pierre Brichard's book of cichlids and other fishes of Lake Tanganyika. TFH Publications,, New Jersey.

Broglio, C., Rodríguez, F., Salas, C., 2003. Spatial cognition and its neural basis in teleost fishes. Fish and fisheries 4, 247–255. https://doi.org/10.1046/j.1467-2979.2003.00128.x.

Bshary, R., Gingins, S., Vail, A.L., 2014. Social cognition in fishes. Trends in Cognitive Sciences 18, 465–471. https://doi.org/10.1016/j.tics.2014.04.005.

Budeau, D.A., Verts, B.J., 1986. Relative brain size and structural complexity of habitats of chipmunks. Journal of Mammalogy 67, 579–581. https://doi.org/10.2307/1381291.

Burkart, J.M., van Schaik, C.P., 2010. Cognitive consequences of cooperative breeding in primates? Animal Cognition 13, 1–19. https://doi.org/10.1007/s10071-009-0263-7.

Burkart, J.M., van Schaik, C.P., 2016. Revisiting the consequences of cooperative breeding. Journal of Zoology 299, 77–83. https://doi.org/10.1111/jzo.12322.

Burns G., J., Rodd, F.H., 2008. Hastiness, brain size and predation regime affect the performance of wild guppies in a spatial memory task. Animal Behaviour 76, 911–922. https://doi.org/10.1016/j.anbehav.2008.02.017.

Byrne, R.W., 1994. The evolution of intelligence. In: Slater, P.J.B., Halliday, T.R. (Eds.), Behaviour and Evolution. Cambridge University Press, United Kingdom, pp. 223–265.

Byrne, R.W., Whiten, A., 1988. Machiavellian intelligence. Oxford University Press,, United Kingdom.

Carbia, P.S., Brown, C., 2019. Environmental enrichment influences spatial learning ability in captive-reared intertidal gobies (*Bathygobius cocosensis*). Animal Cognition 22, 89–98. https://doi.org/10.1007/s10071-018-1225-8.

Christie, M.R., Marine, M.L., French, R.A., Blouin, M.S., 2012. Genetic adaptation to captivity can occur in a single generation. Proceedings of the National Academy of Sciences 109, 238–242. https://doi.org/10.1073/pnas.1111073109.

Costa, S.S., Andrade, R., Carneiro, L.A., Gonçalves, E.J., Kotrschal, K., Oliveira, R.F., 2011. Sex differences in the dorsolateral telencephalon correlate with home range size in blenniid fish. Brain, Behavior and Evolution 77, 55–64. https://doi.org/10.1159/000323668.

Day, J.J., Santini, S., Garcia-Moreno, J., 2007. Phylogenetic relationships of the Lake Tanganyika cichlid tribe Lamprologini: the story from mitochondrial DNA. Molecular Phylogenetics and Evolution 45, 629–642. https://doi.org/10.1016/j.ympev.2007.02.025.

DeCasien, A.R., Williams, S.A., Higham, J.P., 2017. Primate brain size is predicted by diet but not sociality. Nature Ecology & Evolution 1, 1–7. https://doi.org/10.1038/s41559-017-0112.

Desjardins, J.K., Fitzpatrick, J.L., Stiver, K.A., Van der Kraak, G.J., Balshine, S., 2008. Costs and benefits of polygyny in the cichlid *Neolamprologus pulcher*. Animal Behaviour 75, 1771–1779. https://doi.org/10.1016/j.anbehav.2007.09.037.

Dey, C.J., O'Connor, C.M., Wilkinson, H., Shultz, S., Balshine, S., Fitzpatrick, J.L., 2017. Direct benefits and evolutionary transitions to complex societies. Nature Ecology & Evolution 1, 0137. https://doi.org/10.1038/s41559-017-0137.

Doyle, R.W., Talbot, A.J., 1986. Artificial selection on growth and correlated selection on competitive behaviour in fish. Canadian Journal of Fisheries and Aquatic Sciences 43, 1059–1064. https://doi.org/10.1139/f86-132.

Dugatkin, L., 2002. Animal cooperation among unrelated individuals. Naturwissenschaften 89, 533–541. https://doi.org/10.1007/s00114-002-0379-y.

Dunbar, R.I.M., Shultz, S., 2007a. Evolution in the social brain. Science 317, 1344–1347. https://doi.org/10.1126/science.1145463.

Dunbar, R.I., Shultz, S., 2007b. Understanding primate brain evolution. Philosophical Transactions of the Royal Society B: Biological Sciences 362, 649–658. https://doi.org/10.1098/rstb.2006.2001.

Durán, E., Ocaña, F.M., Broglio, C., Rodríguez, F., Salas, C., 2010. Lateral but not medial telencephalic pallium ablation impairs the use of goldfish spatial allocentric strategies in a "hole-board" task. Behavioural Brain Research 214, 480–487. https://doi.org/10.1016/j.bbr.2010.06.010.

Ebbesson, L.O.E., Braithwaite, V.A., 2012. Environmental effects on fish neural plasticity and cognition. Journal of Fish Biology 81, 2151–2174. https://doi.org/10.1111/j.1095-8649.2012.03486.x.

Effenberger, E., Mouton, P.L.F., 2007. Space use in a multi-male group of the group-living lizard. Journal of Zoology 272, 202–208. https://doi.org/10.1111/j.1469-7998.2006.00256.x.

Fagan, W.F., Lewis, M.A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., LaDage, L., Schlägel, U.E., Tang, W.W., Papastamatiou, Y.P., Forester, J., 2013. Spatial memory and animal movement. Ecology Letters 16, 1316–1329. https://doi.org/10.1111/ele.12165.

Fernandez-Baizan, C., Arias, J.L., Mendez, M., 2019. Spatial memory in young adults: Gender differences in egocentric and allocentric performance. Behavioural Brain Research 359, 694–700. https://doi.org/10.1016/j.bbr.2018.09.017.

Flood, N.B., Overmier, J.B., 1981. Learning in teleost fish: role of the telencephalon. In: Laming, P.R. (Ed.), Brain mechanisms of behaviour in lower vertebrates. Cambridge University Press, United Kingdom, pp. 259–279.

Friard, O., Gamba, M., 2016. BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. Methods in Ecology and Evolution 7, 1325–1330. https://doi.org/10.1111/2041-210X.12584.

Fukumori, K., Okuda, N., Yamaoka, K., Yanagisawa, Y., 2010. Remarkable spatial memory in a migratory cardinalfish. Animal Cognition 13, 385–389. https://doi.org/10.1007/s10071-009-0285-1.

Gatto, E., Lucon-Xiccato, T., Bisazza, A., 2018. Factors affecting the measure of inhibitory control in a fish (*Poecilia reticulata*). Behavioural Processes 157, 11–17. https://doi.org/10.1016/j.beproc.2018.08.003.

Geary, D.C., 1995. Sexual selection and sex differences in spatial cognition. Learning and Individual Differences 7, 289–301. https://doi.org/10.1016/1041-6080(95)90003-9.

Girvan, J.R., Braithwaite, V.A., 1998. Population differences in spatial learning in three–spined sticklebacks. Proceedings of the Royal Society of London. Series B: Biological Sciences 265, 913–918. https://doi.org/10.1098/rspb.1998.0378.

Gonda, A., Herczeg, G., Merilä, J., 2009. Adaptive brain size divergence in nine-spined sticklebacks (*Pungitius pungitius*)? Journal of Evolutionary Biology 22, 1721–1726. https://doi.org/10.1111/j.1420-9101.2009.01782.x.

Goodson, J.L., Bass, A.H., 2001. Social behavior functions and related anatomical characteristics of vasotocin/vasopressin systems in vertebrates. Brain Research Reviews 35, 246–265. https://doi.org/10.1016/S0165-0173(01)00043-1.

Hager, M.C., Helfman, G.S., 1991. Safety in numbers: shoal size choice by minnows under predatory threat. Behavioral Ecology and Sociobiology 29, 271–276. https://doi.org/10.1007/BF00163984.

Hewitt, K.N., Boon, W.C., Murata, Y., Jones, M.E., Simpson, E.R., 2003. The aromatase knockout mouse presents with a sexually dimorphic disruption to cholesterol homeostasis. Endocrinology 144, 3895–3903. https://doi.org/10.1210/en.2003-0244.

Hick, K., Reddon, A.R., O'Connor, C.M., Balshine, S., 2014. Strategic and tactical fighting decisions in cichlid fishes with divergent social systems. Behaviour 151, 47–71. https://doi.org/10.1163/1568539X-00003122.

Holekamp, K.E., 2007. Questioning the social intelligence hypothesis. Trends in Cognitive Sciences 11, 65–69. https://doi.org/10.1016/j.tics.2006.11.003.

Huntingford, F.A., 2004. Implications of domestication and rearing conditions for the behaviour of cultivated fishes. Journal of Fish Biology 65, 122–142. https://doi.org/10.1111/j.0022-1112.2004.00562.x.

Huntingford, F.A., Lazarus, J., Barrie, B.D., Webb, S., 1994. A dynamic analysis of cooperative predator inspection in sticklebacks. Animal Behaviour 47, 413–423. https://doi.org/10.1006/anbe.1994.1055.

Iwaniuk, A.N., Arnold, K.E., 2004. Is cooperative breeding associated with bigger brains? A comparative test in the Corvida (Passeriformes). Ethology 110, 203–220. https://doi.org/10.1111/j.1439-0310.2003.00957.x.

Johnson-Ulrich, L., 2017. The Social Intelligence Hypothesis. In: Shackelford, T.K., Weekes-Shackelford, V.A. (Eds.), Encyclopedia of Evolutionary Psychological Science. Springer International Publishing, pp. 1–7.

Kappeler, P.M., 2019. A framework for studying social complexity. Behavioral Ecology and Sociobiology 73, 13. https://doi.org/10.1007/s00265-018-2601-8.

Keenleyside, M.H., 1955. Some aspects of the schooling behaviour of fish. Behaviour 8, 183–247. https://doi.org/10.1163/156853955X00229.

Konings, A., 1998. Tanganyika cichlids in their natural habitat. Cichlid Press,, Texas.

Kotrschal, A., Rogell, B., Maklakov, A.A., Kolm, N., 2012. Sex-specific plasticity in brain morphology depends on social environment of the guppy. Poecilia reticulata. Behavioral Ecology and Sociobiology 66, 1485–1492. https://doi.org/10.1007/s00265-012-1403-7.

Kotrschal, A., Taborsky, B., 2010. Environmental change enhances cognitive abilities in fish. PLoS Biol 8, e1000351. https://doi.org/10.1371/journal.pbio.1000351.

Krause, J., Godin, J.G.J., 1994. Shoal choice in the banded killifish (*Fundulus diaphanus*, Teleostei, Cyprinodontidae): effects of predation risk, fish size, species composition and size of shoals. Ethology 98, 128–136. https://doi.org/10.1111/j.1439-0310.1994.tb01063.x.

Kummer, H., Daston, L., Gigerenzer, G., Silk, J.B., 1997. The Social Intelligence Hypothesis. In: Weingart, P., Mitchell, S.D., Richerson, P.J., Maasen, S. (Eds.), Human by nature: Between biology and the social sciences. Erlbaum, New Jersey, pp. 157–179.

Kutsukake, N., 2009. Complexity, dynamics and diversity of sociality in group-living mammals. Ecological Research 24, 521–531. https://doi.org/10.1007/s11284-008-0563-4.

Li, M., Bolker, B., 2019. wzmli/phyloglmm: First release of phylogenetic comparative analysis in lme4-verse (Version v1.0.0). Zenodo. https://doi.org/10.5281/zenodo.2639887.

Lindenfors, P., Wartel, A., Lind, J., 2021. 'Dunbar's number' deconstructed. Biology Letters 17, 20210158. https://doi.org/10.1098/rsbl.2021.0158.

Livingstone-Lee, S.A., Zeman, P.M., Gillingham, S.T., Skelton, R.W., 2014. Navigational strategy may be more a matter of environment and experience than gender. Learning and Motivation 45, 30–43. https://doi.org/10.1016/j.lmot.2013.09.003.

Lucon-Xiccato, T., Bisazza, A., 2017a. Individual differences in cognition among teleost fishes. Behavioural Processes 141, 184–195. https://doi.org/10.1016/j.beproc.2017.01.015.

Lucon-Xiccato, T., Bisazza, A., 2017b. Sex differences in spatial abilities and cognitive flexibility in the guppy. Animal Behaviour 123, 53–60. https://doi.org/10.1016/j.anbehav.2016.10.026.

Lucon-Xiccato, T., Gatto, E., Bisazza, A., 2017. Fish perform like mammals and birds in inhibitory motor control tasks. Scientific Reports 7, 1–8. https://doi.org/10.1038/s41598-017-13447-4.

Magurran, A.E., Garcia, C.M., 2000. Sex differences in behaviour as an indirect consequence of mating system. Journal of Fish Biology 57, 839–857. https://doi.org/10.1111/j.1095-8649.2000.tb02196.x.

O'Donnell, S., Bulova, S.J., DeLeon, S., Khodak, P., Miller, S., Sulger, E., 2015. Distributed cognition and social brains: reductions in mushroom body investment accompanied the origins of sociality in wasps (Hymenoptera: Vespidae). Proceedings of the Royal Society B: Biological Sciences 282, 20150791. https://doi.org/10.1098/rspb.2015.0791.

O'Connor, C.M., Reddon, A.R., Odetunde, A., Jindal, S., Balshine, S., 2015. Social cichlid fish change behaviour in response to a visual predator stimulus, but not the odour of damaged conspecifics. Behavioural Processes 121, 21–29. https://doi.org/10.1016/j.beproc.2015.10.002.

Pollen, A.A., Dobberfuhl, A.P., Scace, J., Igulu, M.M., Renn, S.C., Shumway, C.A., Hofmann, H.A., 2007. Environmental complexity and social organization sculpt the brain in Lake Tanganyikan cichlid fish. Brain, Behaviour and Evolution 70, 21–39. https://doi.org/10.1159/000101067.

Powell, L.E., Isler, K., Barton, R.A., 2017. Re-evaluating the link between brain size and behavioural ecology in primates. Proceedings of the Royal Society B: Biological Sciences 284, 20171765. https://doi.org/10.1098/rspb.2017.1765.

Pravosudov, V.V., Roth II, T.C., 2013. Cognitive ecology of food hoarding: the evolution of spatial memory and the hippocampus. Annual Review of Ecology, Evolution, and Systematics 44, 173–193. https://doi.org/10.1146/annurev-ecolsys-110512-135904.

R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing,, Vienna, Austria. ⟨http://www.R-project.org⟩.

Reader, S.M., Laland, K.N., 2000. Diffusion of foraging innovations in the guppy. Animal Behaviour 60, 175–180. https://doi.org/10.1006/anbe.2000.1450.

Reader, S.M., Laland, K.N., 2002. Social intelligence, innovation, and enhanced brain size in primates. Proceedings of the National Academy of Sciences 99, 4436–4441. https://doi.org/10.1073/pnas.062041299.

Reddon, A.R., Dey, C.J., Balshine, S., 2019. Submissive behaviour is mediated by sex, social status, relative body size and shelter availability in a social fish. Animal Behaviour 155, 131–139. https://doi.org/10.1016/j.anbehav.2019.06.026.

Reddon, A.R., O'Connor, C.M., Ligocki, I.Y., Hellmann, J.K., Marsh-Rollo, S.E., Hamilton, I.M., Balshine, S., 2016. No evidence for larger brains in cooperatively breeding cichlid fishes. Canadian Journal of Zoology 94, 373–378. https://doi.org/10.1139/cjz-2015-0118.

Reddon, A.R., O'Connor, C.M., Nesjan, E., Cameron, J., Hellmann, J.K., Ligocki, I.Y., Marsh-Rollo, S.E., Hamilton, I.M., Wylie, D.R., Hurd, P.L., Balshine, S., 2017. Isotocin neuronal phenotypes differ among social systems in cichlid fishes. Royal Society Open Science 4, 170350. https://doi.org/10.1098/rsos.170350.

Rhodes, M.E., Rubin, R.T., 1999. Functional sex differences (sexual diergism') of central nervous system cholinergic systems, vasopressin, and hypothalamic–pituitary–adrenal axis activity in mammals: a selective review. Brain Research Reviews 30, 135–152. https://doi.org/10.1016/S0165-0173(99)00011-9.

Riedel, G., 1998. Long-term habituation to spatial novelty in blind cave fish (*Astyanax hubbsi*): role of the telencephalon and its subregions. Learning & Memory, *4* , 451–461. doi:10.1101/lm.4.6.451Learn. Mem. 1998. 4: 451-461.

Rodrıguez, F., López, J.C., Vargas, J.P., Broglio, C., Gómez, Y., Salas, C., 2002. Spatial memory and hippocampal pallium through vertebrate evolution: insights from reptiles and teleost fish. Brain Research Bulletin 57, 499–503. https://doi.org/10.1016/S0361-9230(01)00682-7.

Roy, T., Bhat, A., 2018. Divergences in learning and memory among wild zebrafish: Do sex and body size play a role? Learning & behavior 46, 124–133. https://doi.org/10.3758/s13420-017-0296-8.

Salena, M.G., Balshine, S., 2020. Social memory and quantity discrimination: A cross cichlid species comparison. Canadian Journal of Experimental Psychology/Revue canadienne de psychologie expérimentale 74, 207. https://doi.org/10.1037/cep0000212.

Salena, M.G., Turko, A.J., Singh, A., Pathak, A., Hughes, E., Brown, C., Balshine, S., 2021. Understanding fish cognition: a review and appraisal of current practices. Animal Cognition 1–12. https://doi.org/10.1007/s10071-021-01488-2.

Salvanes, A.G.V., Moberg, O., Ebbesson, L.O., Nilsen, T.O., Jensen, K.H., Braithwaite, V. A., 2013. Environmental enrichment promotes neural plasticity and cognitive ability in fish. Proceedings of the Royal Society B: Biological Sciences 280, 20131331. https://doi.org/10.1098/rspb.2013.1331.

Scace, J., Dobberfuhl, A., Higgins, E., Shumway, C., 2006. Complexity and the evolution of the social brain. InterJournal of Complex Systems *1844*.

Schradin, C., Lamprecht, J., 2002. Causes of female emigration in the group-living cichlid fish *Neolamprologus multifasciatus*. Ethology 108, 237–248. https://doi.org/10.1046/j.1439-0310.2002.00775.x.

Sefc, K.M., 2011. Mating and parental care in Lake Tanganyika's cichlids. *470875* International Journal of Evolutionary Biology. https://doi.org/10.4061/2011/470875.

Solomon, N.G., French, J.A., 1997. Cooperative breeding in mammals. Cambridge University Press,, United Kingdom.

Strand, D.A., Utne-Palm, A.C., Jakobsen, P.J., Braithwaite, V.A., Jensen, K.H., Salvanes, A.G., 2010. Enrichment promotes learning in fish. Marine Ecology Progress Series 412, 273–282. https://doi.org/10.3354/meps08682.

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, 2974–2984. https://doi.org/10.1111/j.1365-294X.2007.03350.x.

Stiver, K.A., Fitzpatrick, J., Desjardins, J.K., Balshine, S., 2006. Sex differences in rates of territory joining and inheritance in a cooperatively breeding cichlid fish. Animal Behaviour 7, 449–456. https://doi.org/10.1016/j.anbehav.2005.06.011.

Svensson, P.A., Barber, I., Forsgren, E., 2000. Shoaling behaviour of the two-spotted goby. Journal of Fish Biology 56, 1477–1487. https://doi.org/10.1111/j.1095-8649.2000.tb02158.x.

Thornton, A., McAuliffe, K., 2015. Cognitive consequences of cooperative breeding? A critical appraisal. Journal of Zoology 295, 12–22. https://doi.org/10.1111/jzo.12198.

van Horik, J., Emery, N.J., 2011. Evolution of cognition. Wiley Interdisciplinary Reviews: Cognitive Science 2, 621–633. https://doi.org/10.1002/wcs.144.

Vargas, J.P., López, J.C., Portavella, M., 2009. What are the functions of fish brain pallium? Brain Research Bulletin 79, 436–440. https://doi.org/10.1016/j.brainresbull.2009.05.008.

Wallace, K.J., Hofmann, H.A., 2021. Equal performance but distinct behaviors: sex differences in a novel object recognition task and spatial maze in a highly social cichlid fish. Animal Cognition 1–17. https://doi.org/10.1007/s10071-021-01498-0.

Ward, A., Webster, M., 2016. Sociality: The Behaviour of Group-Living Animals. Springer International Publishing,.

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

West, S.A., Griffin, A.S., Gardner, A., 2007. Evolutionary explanations for cooperation. Current Biology 17, R661–R672. https://doi.org/10.1016/j.cub.2007.06.004.

White, G.E., Brown, C., 2015. Microhabitat use affects brain size and structure in intertidal gobies. Brain, Behavior and Evolution 85, 107–116. https://doi.org/10.1159/000380875.

Whiten, A., Byrne, R.W., 1997. Machiavellian Intelligence II: Extensions and Evaluations. Cambridge University Press,, United Kingdom.

Whiten, A., 2000. Social complexity and social intelligence. In: Bock, G., Goode, J., Webb, K. (Eds.), The nature of intelligence. Wiley, Chichester, pp. 185–201.

Wong, M.Y., Jordan, L.A., Marsh-Rollo, S., St-Cyr, S., Reynolds, J.O., Stiver, K.A., Desjardins, J.K., Fitzpatrick, J.L., Balshine, S., 2012. Mating systems in cooperative breeders: the roles of resource dispersion and conflict mitigation. Behavioral Ecology 23, 521–530. https://doi.org/10.1093/beheco/arr218.

Zakon, H., 2000. Sex steroids and weakly electric fish: a model system for activational mechanisms of hormone action. In: Matsumoto, A. (Ed.), Sexual differentiation of the brain. CRC Press, Florida, pp. 95–112.