



Learning performance is associated with social preferences in a group-living fish

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ABSTRACT

Many animals live in groups yet grouping tendencies and preferences for groups of different sizes vary considerably between individuals. This variation reflects, at least in part, differences in how individuals evaluate and perceive their physical surroundings and their social environment. While such differences are likely related to individual variation in cognition, there have been few studies that have directly investigated how cognitive abilities are linked to individual grouping decisions. Therefore, in this study we assessed whether performance on a foraging-based reversal learning task is related to grouping preferences (a group of three fish versus a single fish) in a group-living cichlid fish, *Neolamprologus pulcher*. While most fish preferred to associate with the group over a single fish, individuals that completed the reversal learning task the quickest were the least interested in the group under elevated predation risk. In addition, fish that quickly completed the reversal learning task also adjusted their grouping preferences the most when predation risk increased. This result suggests that the observed relationship between learning performance and grouping decisions may be linked to individual differences in behavioural flexibility. Overall, our results offer valuable insight into the potential factors that underlie inter-individual variation in grouping decisions.

1. Introduction

Group-living confers many benefits to group members, including reduced predation risk (Hamilton, 1971; Landeau and Terborgh, 1986; Wrona and Dixon, 1991), workload sharing (Dornhaus et al., 2008; Ulrich et al., 2018), improved foraging (Evans et al., 2016; Ward and Zahavi, 1973), and enhanced transmission of information (Aplin and Morand-Ferron, 2017; Kulahci et al., 2018). However, living in a group can also be costly to individuals because groups are often more conspicuous to predators (Cresswell and Quinn, 2011; Wrona and Dixon, 1991), and group members can face increased competition over limited resources (Cant et al., 2006; Janson and Goldsmith, 1995) and a higher risk of parasite/disease transmission (Brown and Brown, 1986; Cote and Poulin, 1995). However, the costs and benefits of grouping can fluctuate over time as resource availability and predation risk change in the surrounding environment (Fortin and Fortin, 2009; Hoare et al., 2004). Hence, deciding whether or not to join a group and choosing what size and composition of group to join are complex decisions that can have lasting effects on an individual's physiology, health, and overall fitness (Markham et al., 2015; Sapolsky, 2005; Shreeves and Field, 2002).

Grouping decisions are largely dependent on how individuals evaluate and perceive both the state of their surrounding environment, as well as the various trade-offs associated with different grouping options (Metcalf and Thomson, 1995; Reddon et al., 2011). Some individuals will more accurately perceive and assess these costs and benefits. Therefore, it is likely that grouping decisions reflect in part individual differences in cognition and decision making (Crony and Newberry, 2007; Wascher et al., 2018). For example, while some individuals rely on observing and interacting with older, more experienced group members to acquire information and resources (*i.e.*, social learning), others are less reliant on group members as a source of information and instead acquire information on their own (*i.e.*, individual learning; Galef and Laland 2005; Mesoudi et al. 2016). Therefore, grouping decisions can be influenced by learning ability where better individual learners might be more inclined to join small groups to avoid the high levels of intragroup competition associated with living in a large group (Aplin and Morand-Ferron, 2017; Katsnelson et al., 2011). However, if environmental conditions change and the benefits of large groups begin to outweigh the costs (*e.g.*, under high predation risk; Kendal et al. 2005), then all individuals may be expected to prefer larger groups. Although,

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there is considerable variation in the extent that individuals can adjust their behaviour (Coppens et al., 2010; Dougherty and Guillette, 2018; Sih and Del Giudice, 2012) and some individuals do not adjust their behaviour irrespective of changes in their surrounding environment (Wolf et al., 2008, 2011). Consequently, an individual's relative behavioural flexibility is also likely to be an important factor when considering social responses following environmental perturbations.

In general, cognition is thought to be under strong selection in highly social animals because of the cognitive demands that typically come with group-living (Dávid-Barrett and Dunbar, 2013; Wascher et al., 2018). Cognitive skills related to social interactions such as recognizing different individuals and rapidly resolving disputes are especially important aptitudes for animals that live in complex societies where individuals must develop and maintain long-term, individuated social relationships with both groupmates and neighbours alike (Wascher et al., 2018). Highly social animals also often have enhanced general cognitive skills, including individual learning (Borrego and Gaines, 2016; Costanzo et al., 2009), transitive inference (Bond et al., 2010; MacLean et al., 2008) and behavioural flexibility (Amici et al., 2008; Ashton et al., 2018; Johnson-Ulrich and Holekamp, 2020). However, while convincing evidence of the relationship between cognition and sociality exists for birds (Aplin and Morand-Ferron, 2017; Ashton et al., 2018; Langley et al., 2020; Wascher, 2015), mammals (Johnson-Ulrich and Holekamp, 2020; Kulahci et al., 2018; MacLean et al., 2013), and fishes (Chapman et al., 2008; Etheredge et al., 2018), few studies have directly investigated how cognitive performance relates to grouping decisions in the face of fluctuating environmental conditions. Therefore, the aim of the current study was to determine how the relationship between learning performance and group preferences is modulated by variation in predation risk.

To assess this, we used *Neolamprologus pulcher*—a cooperatively breeding cichlid fish from Lake Tanganyika in Africa. These fish live in social groups consisting of a dominant female-male breeding pair and between 1–20 subordinate helpers (Balshine et al., 2001; Heg et al., 2005), and larger groups are generally more stable and resilient to disturbances (Anderson et al., 2020; Heg et al., 2005). Individuals occasionally move between groups (Bergmüller et al., 2005; Dierkes et al., 2005; Hellmann et al., 2016; Stiver et al., 2007; Stiver et al., 2006) and fish strongly prefer to join larger groups (Reddon et al., 2011; Salena and Balshine, 2020); likely because individuals in large groups tend to have a lower workload and reduced risk of predation (Balshine et al., 2001; Heg et al., 2004a; Jungwirth et al., 2015). However, *N. pulcher* groups are structured in a linear, size-based dominance hierarchy (Dey et al., 2013; Wong and Balshine, 2011) in which dominants restrict subordinate growth and reproduction via aggressive acts (Fitzpatrick et al., 2006; Heg et al., 2004b; Hellmann et al., 2015). Consequently, joining a large group can delay or even reduce an individual's overall reproductive output. Therefore, group-joining decisions in *N. pulcher* are complex and the outcome of these decisions likely depends on individual differences in cognitive capacity.

To determine whether grouping decisions reflect individual differences in cognition, we assessed how performance on a foraging-based reversal learning task related to grouping preferences (a group of three fish versus a single fish) in the absence or presence of a predator. We hypothesized that individuals that completed the reversal learning task faster would prefer to associate with smaller groups because fast reversal learners can reliably produce information on their own, thereby allowing them to avoid the high levels of competition that can occur in large groups. Based on this hypothesis, we predicted that performance on the reversal learning assay would be negatively related to the preference of individuals for the larger group. An alternative hypothesis is that individuals completing the reversal learning task faster may be better at capitalizing on information acquired from groupmates, and so will prefer larger groups because they offer more opportunities to acquire information socially—especially under predation risk when producing information on your own can be costly (Laland, 2004).

Additionally, because reversal learning is thought to reflect behavioural flexibility (i.e., old associations must be forgotten and new associations formed; Izquierdo et al., 2017; Lai et al., 1995), we also hypothesized that fast reversal learners would be more responsive to changes in their environment. Therefore, we predicted that fish that more quickly learned to choose a previously unrewarded option over a previously rewarded option during the reversal learning task would also be more likely to adjust their grouping preferences when predation risk changed (i.e., behavioural flexibility is consistent across contexts).

2. Methods

2.1. Experimental Animals

Experiments were conducted from January–April 2018 using laboratory-reared *N. pulcher* that were ~3rd generation descendants of wild breeding pairs that were caught in Lake Tanganyika along the coastline of northern Zambia. Prior to experimentation fish were held in 527 L stock tanks containing ~75 adults of mixed sex. All aquaria were held at 27 °C and a 13:11 h light:dark photoperiod was maintained. Fish were observed daily to monitor their condition and health, and were fed ad libitum once a day, 6 days per week with commercial cichlid flakes prior to the experiment.

2.2. Experimental Protocols

2.2.1. Reversal Learning Assay

At the start of the experiment, all fish (N = 24; 14 females, 10 males) were sexed by examination of their genital papillae and measured for standard length (mean ± SEM of 5.1 ± 0.1 cm). Fish were then placed individually into 38 L aquaria containing a heater, air stone, mechanical filter, flower pot half, 3 cm of coral sand for substrate, and a small, white plastic feeding tray with 10 wells (2 rows of 5; 9 mm diameter, 7 mm depth).

After a 24-h acclimation period, bloodworms were placed on the tray to encourage fish to associate the tray with food. Fish were then trained to move a small, plastic disc to access a food reward from one of the tray's wells (Fig. 1A). Fish were trained using either blue (N = 12; 7 females and 5 males) or yellow discs (N = 12; 7 females and 5 males) and performed 10 trials per day until they had successfully accessed the food reward from a completely covered well in three consecutive trials (up to a maximum of 50 trials). One fish failed to meet this criterion, so it was excluded from the experiment and returned to the stock tank.

Following the initial training phase, we tested whether fish had successfully learned to associate a food reward with the coloured disc that they were previously trained on. Fish were presented with two discs each of a different colour (i.e., one disc was the familiar colour and the other disc was a novel colour) on the feeding tray with bloodworms hidden underneath both discs to prevent differences in olfactory cues. The coloured disc that fish were previously trained on (and were familiar with) remained accessible, while the novel coloured disc was inaccessible (a steel nut that fit snugly into the well was affixed to the bottom of the disc to prevent the disc from being moved). The location of the two discs on the food tray was selected randomly using a random number generator. We then monitored which disc the fish first attempted to dislodge over 10 trials per day for a total of two days (20 trials). During this time all but one fish successfully learned to associate the previously rewarded coloured disc with food (8 correct choices over 10 consecutive trials). This fish was excluded from the experiment and it was returned to the stock tank.

Lastly, we conducted a reversal learning task where we switched which coloured discs were accessible versus inaccessible. Reversal learning tasks are generally considered to be more challenging and require greater flexibility than standard associative learning tasks (Izquierdo et al., 2017; Lai et al., 1995) because old associations need to be forgotten and new associations formed. Therefore, in this reversal

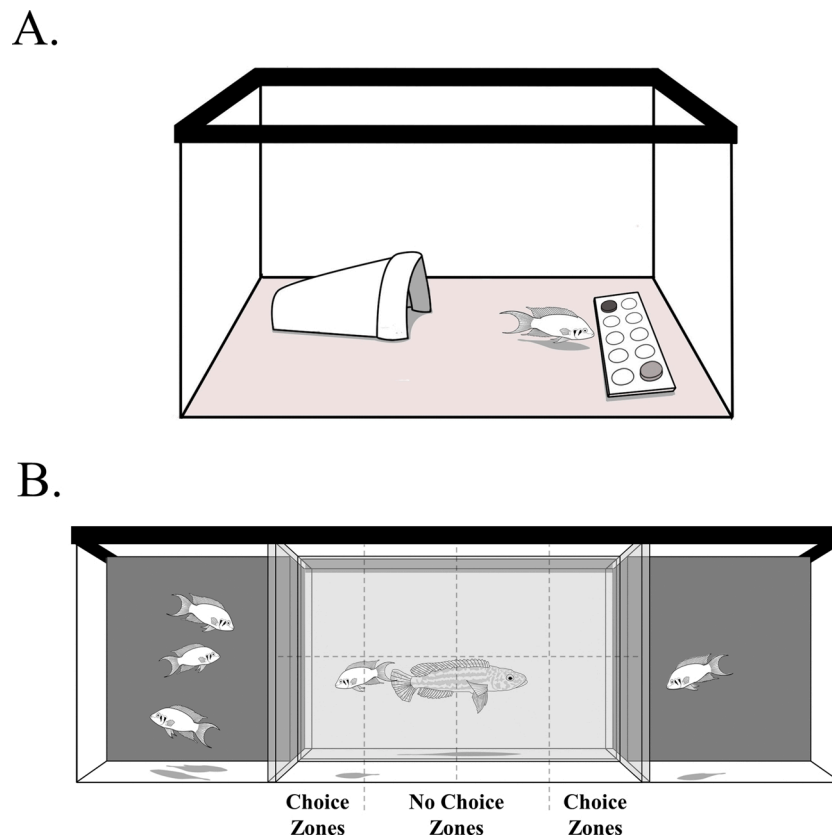


Fig. 1. Illustrations of the experimental set-ups used for A) the learning task in Experiment 1 and B) the social preference assay in Experiment 2. Focal fish exhibited a social preference when they were in either of the choice zones located on the sides of their central compartment.

learning task we assessed which disc fish first attempted to dislodge over ten trials per day for a total of six days (60 trials).

2.2.2. Grouping Preferences Assay

The morning after the final reversal learning trial (between 900 and 1400 h) we assessed the grouping preferences of each fish (Fig. 1B). Focal fish were gently guided into a clear plastic tube (height = 32 cm; diameter = 11 cm) and transferred into a 189 L tank that had been divided into 6 compartments. Each compartment was separated by non-perforated, opaque dividers and contained 3 cm of crushed coral sand as substrate. The tube containing the focal fish was placed in the anterior, middle compartment. On both sides of the focal fish's compartment were compartments that contained either three fish (a dominant male, dominant female, and helper from a previously established social group) or a single fish (a stock tank fish that was sex-matched with the focal fish). Stimuli fish were replaced between every trial so that each focal fish had a unique set of stimuli fish to choose between and the side of the tank on which stimuli fish (a group versus a singleton) were placed was alternated between trials. All stimuli fish were at least 5% larger in standard length than the focal fish. The posterior, middle compartment contained a separate aquarium (to prevent olfactory cues) that held a single *Lepidolamprologus kendalli* ($N = 3$; $SL = 8.3 \pm 0.2$ cm) which was visible only to the focal fish. *L. kendalli* are a piscivorous, predatory cichlid native to Lake Tanganyika that can kill small *N. pulcher* and injure larger fish (Heg et al., 2004a; Konings, 2019). Predators were exchanged between each trial to avoid exhaustion. The posterior side compartments were both empty.

Each focal fish ($N = 22$) underwent a single trial that lasted a total of 30 min and was recorded using a Canon VIXIA HF S200 video camera. Each trial began with a 5 min acclimation period, following which the tube containing the focal fish was remotely raised and fish were given 5 min to explore their surroundings. At the end of this exploration period,

the opaque barriers which separated the focal fish from the conspecific stimuli compartments were raised and each focal fish was able to interact with the stimuli fish across non-perforated, clear dividers. After 10 min of interaction, the posterior opaque divider was raised to reveal the *L. kendalli* predator stimuli. Fish interacted for another 10 min in the presence of the predator, after which trials were concluded and fish were returned to their respective tanks. We remotely monitored each trial to ensure that fish did not display any signs of distress. All trials were conducted in the same order to ensure that focal fish behaviour in the absence of the predator was not influenced by carryover effects owing to prior predator interactions (Bell and Sih, 2007; Niemelä et al., 2012; Thomson et al., 2012).

All videos were scored by a single observer that was blind to the identity of each focal fish (NT). To assess social preferences, the middle compartment containing the focal fish was divided into eight equal sections (2 rows of 4; see Fig. 1B). We measured the amount of time that the focal fish spent in the “choice” zones (the two sections next to the compartments containing the stimuli fish) beside the group of three fish versus the time spent in the “choice” zones nearest to the single fish. Focal fish were scored as being in a particular section if their operculum was in that section (i.e., had crossed the line). If the focal fish was in the “no choice” zones (four middle sections) then it was considered to not be displaying a preference at that time. We also measured the amount of time that focal fish spent in the upper versus lower half of the aquarium (a measure of anxiety/fear—the upper portion of the water column presents a higher risk of predation and more anxious/fearful fish spend less time here (Angiulli et al., 2020; Simmons et al., 2017)), the total number of times that fish transitioned between sections (a measure of locomotor activity), and the total proportion of unique sections that fish entered (a measure of exploration). These same measures were recorded during the 10 min periods when the predator was absent and present.

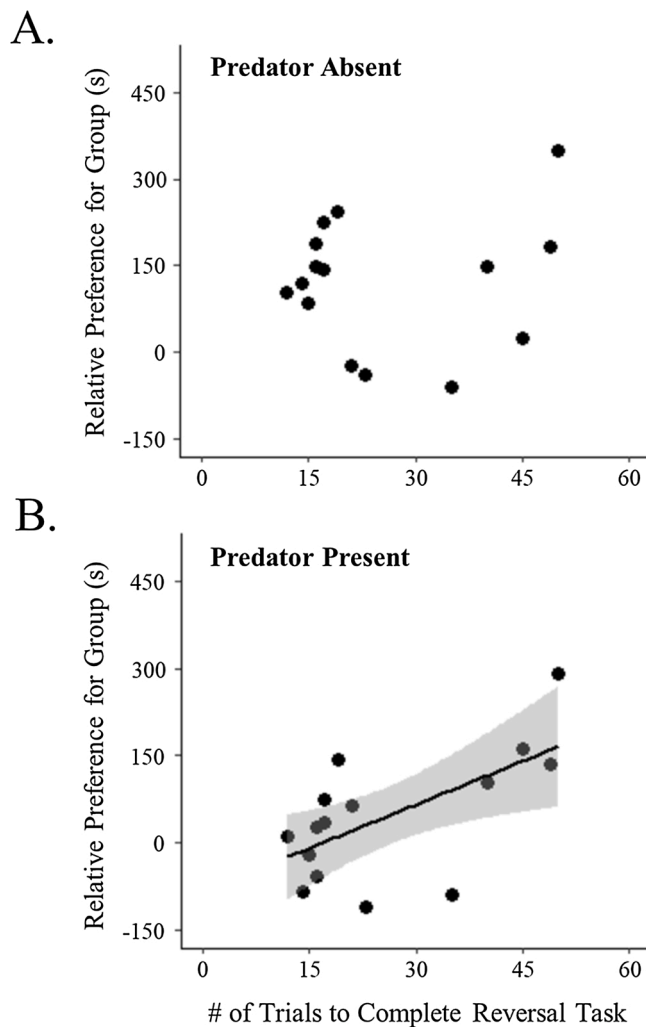


Fig. 2. Relationship between the number of trials required to accomplish the reversal learning task and relative group preferences of individual *N. pulcher* ($N = 15$) when a predator was absent (A) or present (B). Performance on the reversal learning task did not relate to grouping preferences in the absence of a predator ($p = 0.48$), but fish that completed the reversal learning task more quickly displayed less of a preference for the group of three fish when the predator was present ($p = 0.02$). A linear regression was fit for the significant relationship only; the shaded area represents the 95% confidence interval of the regression line.

2.3. Statistical Analysis

We used an 80% accuracy criterion (8 correct choices over 10 consecutive trials during the reversal portion of the learning assay) to determine when fish had successfully accomplished the reversal learning task. We have focused our analysis on individuals that

Table 1

Results of linear models assessing how relative group preferences when a predator was either absent or present related to performance on the reversal learning task ($N = 15$). Significant results ($p < 0.05$) are depicted in **bold**. See text for full description of the statistical analyses.

		Estimate \pm SEM	F	p	R ²
Relative Group Preferences (Predator Absent)	# of Trials	2.47 \pm 2.87	0.53	0.48	0.08
	Sex	248.63 \pm 270.04	0.44	0.52	
	# of Trials * Sex	-11.29 \pm 14.75	0.59	0.46	
Relative Group Preferences (Predator Present)	# of Trials	6.43 \pm 2.13	8.11	0.02	0.42
	Sex	265.66 \pm 200.82	0.69	0.42	
	# of Trials * Sex	-12.44 \pm 10.97	1.29	0.28	

successfully met this criterion ($N = 15$) and have removed all individuals that failed to successfully complete any portion of the learning assay ($N = 9$).

Statistical analyses were performed using R (v. 3.6.3, R Core Team, 2021) and a significance level (α) of 0.05 was used for all tests. All models were fit using the ‘lme4’ package (Bates et al., 2015) and overall differences were evaluated using the ‘Anova’ function in the ‘car’ package (Fox and Weisberg, 2011). The assumptions of all models were evaluated visually using the ‘performance’ package (Lüdtke et al., 2021). We also calculated R² values for all linear models (LMs), as well as marginal (proportion of variation explained by the fixed effects alone) and conditional (combined proportion of variation explained by the fixed and random effects) R² values for all linear mixed-effect models (LMMs) (Nakagawa et al., 2017; Nakagawa and Schielzeth, 2013) using the ‘MuMIn’ package (Barton, 2020).

We initially assessed whether group preferences of focal fish (time-group of 3 fish - time_{single fish}) in either the presence or absence of a predator related to their performance on the reversal learning task using LMs. Models included the number of trials required to reach the 80% accuracy criterion during the reversal learning task, focal fish sex (male or female), and their interaction term as fixed factors. While we have previously found that disc colour influences performance curves during learning assays in *N. pulcher* (Culbert et al., 2020), the inclusion of disc colour as a random effect did not improve the fit or the outcome of the models reported here and was therefore not included in our final models.

We also evaluated how focal fish behaviour (group preferences, overall time spent with conspecifics, anxiety/fear, activity, and exploration) changed in response to increased predation risk using LMMs. These models included predation risk (predator absent or present), focal fish sex (male or female), and their interaction term as fixed factors, with individual id as a random factor. In addition, we assessed whether group preferences changed over the course of either interaction period (with and without the predator visible) using LMMs that included the portion of the interaction period (initial 5 min or final 5 min), focal fish sex (male or female), and their interaction term as fixed factors, with individual id as a random factor.

Lastly, we assessed whether the absolute change in focal fish grouping preferences following predator introduction ($|\text{group preference}_{\text{predator absent}} - \text{group preference}_{\text{predator present}}|$) related to their performance on the reversal learning task using a LM that included the number of trials required to reach the 80% accuracy criterion during the reversal learning task, focal fish sex (male or female), and their interaction term as fixed factors.

3. Results

3.1. Did grouping decisions relate to performance on the reversal learning task?

Fish that successfully completed the reversal learning assay did so in 25.9 ± 3.6 trials (AVG \pm SEM; Range = 12-49 trials). Group preferences in the absence of a predator were not related to how quickly focal fish completed the reversal learning task (Fig. 2A; $F = 0.53$, $p = 0.48$), but

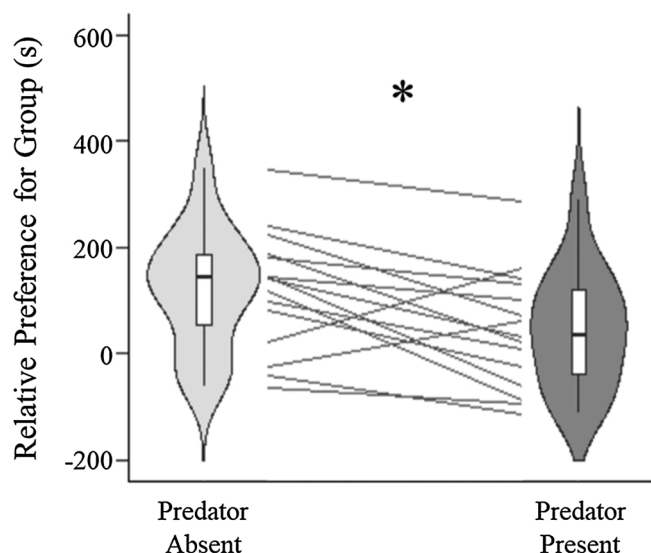


Fig. 3. Differences in relative group preferences of individual *N. pulcher* (N = 15) in the absence (light grey) or presence of a predator (dark grey). Values are presented as medians, 1 st and 3rd quartiles, and 1.5X the interquartile range; lines represent individual responses. The distribution of the data is depicted by the relative width of the coloured portions of each plot. An asterisk is used to indicate that fish reduced their preference for the group of three fish when a predator was introduced ($p = 0.001$).

fish that completed the reversal learning task more quickly displayed a weaker preference for the group when the predator was present (Fig. 2B; $F = 8.11$, $p = 0.02$). No other significant relationships or interactions were observed (Table 1).

3.2. How did individual behaviour change following predator exposure?

In the absence of a predator, fish spent approximately twice as much time with the group of three fish versus a single fish, but surprisingly fish reduced their preference for the group by ~60% (Fig. 3; $X^2 = 10.32$, $p = 0.001$) and spent ~30% less time with conspecifics overall ($X^2 = 19.90$, $p < 0.001$) after the predator was revealed. However, fish were more anxious/fearful when predation risk increased, spending ~20% less time in the upper half of the tank compared to when the predator was

Table 2

Results of linear mixed-effect models evaluating changes in behaviour following predator introduction (N = 15). Significant results ($p < 0.05$) are depicted in **bold**. Marginal (proportion of variation explained by the fixed effects alone) and conditional (combined proportion of variation explained by the fixed and random effects) R^2 values are reported for all models. See text for full description of the statistical analyses.

		Estimate ± SEM	X^2	p	R^2_{Marginal}	$R^2_{\text{Conditional}}$
Change in Group Preferences	Predator	-52.56 ± 30.99	10.32	0.001	0.12	0.71
	Sex	19.89 ± 60.51	0.04	0.85		
	Predator * Sex	-61.44 ± 49.00	1.57	0.21		
Change in Overall Time Spent with Conspecifics	Predator	-119.67 ± 36.45	19.90	<0.001	0.37	0.51
	Sex	-27.67 ± 46.13	0.97	0.32		
	Predator * Sex	-15.67 ± 57.63	0.07	0.79		
Change in Anxiety	Predator	-69.89 ± 44.72	4.35	0.04	0.12	0.36
	Sex	37.83 ± 58.67	0.56	0.46		
	Predator * Sex	-5.78 ± 70.70	0.01	0.94		
Change in Activity	Predator	2.22 ± 5.37	0.70	0.41	0.12	0.71
	Sex	12.56 ± 10.37	2.22	0.14		
	Predator * Sex	3.11 ± 8.49	0.13	0.71		
Change in Exploration	Predator	0.33 ± 0.20	2.96	0.08	0.08	0.28
	Sex	-0.06 ± 0.32	0.05	0.82		
	Predator * Sex	0.01 ± 0.40	0.01	0.99		

not visible ($X^2 = 4.35$, $p = 0.04$). Fish did not adjust their overall activity levels ($X^2 = 0.70$, $p = 0.41$) or the proportion of the tank that they explored after the predator was introduced ($X^2 = 2.96$, $p = 0.08$). Group preferences of individual fish did not change over the course of either interaction period (predator absent: $X^2 = 1.01$, $p = 0.32$; predator present: $X^2 = 1.99$, $p = 0.16$). There were no sex or sex by predation risk interactions (Tables 2 and 3).

3.3. Did changes in grouping decisions following predator exposure relate to performance on the reversal learning task?

Fish that quickly completed the reversal learning task also adjusted their grouping preferences the most following the introduction of a predator (Fig. 4; $F = 6.91$, $p = 0.02$). This relationship was not affected by focal fish sex or the interaction between sex and performance on the reversal learning task (Table 4).

4. Discussion

Fish that completed a reversal learning task more quickly had weaker preferences for a larger group under predation risk suggesting that grouping decisions may be linked to individual differences in cognitive abilities. Additionally, fish that completed the reversal learning task more quickly also adjusted their grouping preferences the most following the introduction of a predator. As such, individual differences in behavioural flexibility appear to be consistent across social and cognitive domains in *N. pulcher*.

Social decisions can have long-lasting effects on an individual's fitness (Markham et al., 2015; Shreeves and Field, 2002); however, the consequences of these decisions typically vary based on individual differences in behaviour and cognition (Crony and Newberry, 2007; Wascher et al., 2018). In the current study, we found that grouping decisions were indeed related to an individual's cognitive performance, as faster reversal learners spent comparatively less time with a group of three fish versus a single fish in the presence of a predator. These results are consistent with the hypothesis that faster reversal learners are less reliant on conspecifics as a source of information and therefore might prefer small groups to avoid high levels of intragroup competition. Similar findings have been reported in wild great tits (*Parus major*; Aplin and Morand-Ferron, 2017), where slower individual learners resided in larger groups and scrounged information from groupmates. As such, cognitive abilities may shape grouping options especially for poor

Table 3

Results of linear mixed-effect models assessing changes in group preferences over the course of the interaction periods in either the absence or presence of a predator (N = 15). Marginal (proportion of variation explained by the fixed effects alone) and conditional (combined proportion of variation explained by the fixed and random effects) R² values are reported for all models. See text for full description of the statistical analyses.

		Estimate ± SEM	X ²	p	R ² _{Marginal}	R ² _{Conditional}
Change in Group Preferences During the Predator Absent Period	1 st or 2 nd Half of Interaction Period	-16.33 ± 41.44	1.01	0.32	0.04	0.20
	Sex	12.83 ± 50.72	0.03	0.86		
	Portion * Sex	-39.67 ± 65.52	0.37	0.55		
Change in Group Preferences During Predator Present Period	1 st or 2 nd Half of Interaction Period	-26.11 ± 33.14	1.99	0.16	0.08	0.19
	Sex	-8.17 ± 39.61	0.48	0.48		
	Portion * Sex	-25.22 ± 52.41	0.63	0.63		

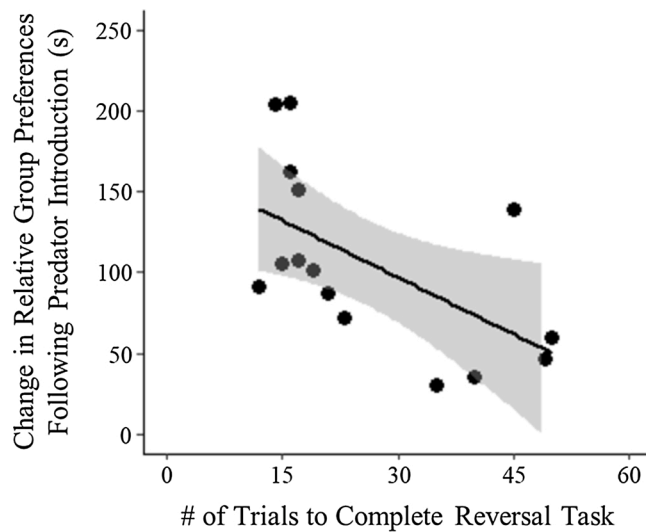


Fig. 4. Relationship between the number of trials required to accomplish the reversal learning task and the absolute change in relative group preferences of individual *N. pulcher* (N = 15) when a predator was introduced. Fish that completed the reversal learning task more quickly adjusted their preference for the group of three fish the most when the predator was introduced (p = 0.02). A linear regression was fit; the shaded area represents the 95% confidence interval of the regression line.

individual learners because they may do best to reside in large groups that are more conducive for social learning and/or information scrounging. However, learning performance in both guppies (*Poecilia reticulata*; Chapman et al., 2008; Kniel et al., 2020) and mosquitofish (*Gambusia affinis*; Etheredge et al., 2018) was positively associated with social preferences for a group versus being alone, while no relationship was observed in ninespine sticklebacks (*Pungitius pungitius*; Webster and Laland, 2015). Under these extreme ‘all-or-none’ conditions, the many benefits associated with being in a group versus being socially isolated likely strongly influenced this relationship and may explain the differences between these studies and our results where fish were offered the more subtle social choice of grouping with either one or three fish. Additionally, these other species live in loosely-structured shoals that mainly serve to reduce predation (Ioannou et al., 2017; Kozak and Boughman, 2012; Pyke, 2005; Seghers, 1974), whereas *N. pulcher* live in

Table 4

Results of linear models assessing how absolute changes in relative group preferences following the introduction of a predator related to performance on the reversal learning task (N = 15). Significant results (p < 0.05) are depicted in **bold**. See text for full description of the statistical analyses.

		Estimate ± SEM	F	p	R ²
Absolute Change in Group Preference Following Predator Introduction	# of Trials	-3.02 ± 1.17	6.91	0.02	0.34
	Sex	-36.25 ± 109.81	1.09	0.32	
	# of Trials * Sex	0.22 ± 6.00	0.01	0.97	

permanent, bonded social groups in which individuals maintain individuated relationships and cooperate to maintain and defend a territory, as well as raise young (Taborsky, 1984; Taborsky and Limberger, 1981; Wong and Balshine, 2011). Consequently, the differences in the function and importance of grouping between these species may also explain these contrasting findings. Indeed, a recent meta-analysis by Dougherty and Guillette (2018) found that the relationship between cognition and sociality varied widely across species; however, they were unable to identify any specific ecological and/or evolutionary factor(s) driving this variation.

The observed negative relationship between group preferences and performance on the reversal learning task was only apparent when grouping preferences were assessed under predation risk. Previous studies have reported that individuals that are bolder under predation risk are also quicker to complete associative learning tasks (Bensky et al., 2017; Carazo et al., 2014; Dugatkin and Alfieri, 2003; reviewed by Dougherty and Guillette, 2018). Our results suggest that a similar relationship may exist between boldness under predation risk and performance on reversal learning tasks. Faster reversal learners spent less time with a group in the presence of a predator in our study, which suggests increased boldness because joining a group is a safer choice under predation risk (Evans et al., 2016; Wrona and Dixon, 1991). However, future studies should directly evaluate this relationship to help broaden our understanding of the relationship between sociality, cognition, and behavioural flexibility.

Visual cues of predation risk elicit strong behavioural responses in *N. pulcher* (Fischer et al., 2017; O'Connor et al., 2015) and fish in our study became more anxious/fearful when a predator was visible, suggesting that they perceived the predator as a threat (Cachat et al., 2011; O'Connor et al., 2015; Thompson et al., 2016). However, focal fish unexpectedly reduced their grouping preferences and spent less time with conspecifics overall under predation risk. These findings differ from the results of O'Connor et al. (2015), which found that *N. pulcher* do not adjust their grouping preferences but spend more overall time with conspecifics under predation risk. These contrasting results likely reflect differences in the size of focal individuals used in the two studies (5.1 cm adults in the current study versus 3.7 cm subadults in the O'Connor et al., 2015 study). While predatory cichlids—like *L. kendalli*—can potentially injure adult *N. pulcher*, they represent a greater threat to smaller, subadult fish (Gashagaza, 1986; Heg et al., 2004a; Hellig et al., 2010; Taborsky, 1985). When predation risk was experimentally elevated in wild social groups of *N. pulcher*, larger

helpers performed more aggression towards predators and spent less time hiding compared to smaller helpers (Heg et al., 2004; Heg and Taborsky, 2010). Therefore, while subadults in O'Connor et al. (2015) may have tried to reduce their risk of predation by being more affiliative, it is possible that the adult fish in our study instead spent more time inspecting and/or confronting the predatory intruder.

Alternatively, the observed reduction in grouping preferences under predation risk may instead reflect a decreased motivation to group across time. While we conducted trials in a standardized order to assure that focal fish behaviour in the absence of the predator was not influenced by carryover effects owing to prior predator interactions (Bell and Sih, 2007; Niemelä et al., 2012; Thomson et al., 2012), this meant that grouping decisions in the presence of the predator always occurred following decisions made in the absence of a predator. Therefore, focal fish may have learned that they could not physically interact with the stimuli fish and gradually lost interest. While such effects have been observed in other studies (Griffiths and Magurran, 1997; Krause et al., 1998; Thünken et al., 2014), previous research with *N. pulcher* suggest that individual grouping decisions occur rapidly (<5 min) and remain consistent across time (>60 min) under benign conditions (Reddon et al., 2011; Reddon et al., 2014). Indeed, individual grouping preferences in the current study did not change during either interaction period (but did change between interaction periods) suggesting that the observed responses to varying predation risk are unlikely to simply reflect motivational changes across time.

In conclusion, our results indicate that grouping preferences may be related to individual differences in learning performance. Additionally, the relative flexibility of individual behaviour appeared to—at least partially—explain the relationship between these cognitive and social tasks. Together, these findings highlight the important relationship between cognition and social decision-making and offer insight into the underlying causes of individual variation in grouping tendencies.

Data accessibility

Supporting data are available as a supplemental file.

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CRedit authorship contribution statement

Brett M. Culbert: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing. **Nicholas Tsui:** Formal analysis, Writing - review & editing. **Sigal Balshine:** Conceptualization, Methodology, Resources, Writing - review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare no competing interests.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.beproc.2021.104464>.

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