Group (reversal) learning is associated with exploration levels in three-spined sticklebacks.

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An individual`s exploration tendency is related to the willingness to expose oneself to potentially dangerous situations in exchange for potential gain. Recently, researchers have linked personality traits to cognitive abilities suggesting that, high exploratory individuals learn faster but are less flexible in learning new cues compared to low exploratory individuals. So far research has focused on individual learning capacity related to personality, however individuals often live in social group and therefore here we studied the effects of group composition on group performance in a foraging task. We screened individual three-spined sticklebacks (*Gasterosteus aculeatus)* for exploration and subsequently assigned them to low, mixed or high exploration groups. These groups were then subjected to a Y-maze learning task, where they learned the location of a food patch. The baited arm was switched after 12 initial learning trials to study reversal learning. We found that, the high exploration groups were faster in finding the baited arm, but were not more correct in their initial choice to enter the baited arm. During reversal learning all groups were slower in finding the baited arm and worse in their initial choice. Especially the high exploratory groups showed a significantly larger increase in the latency to find the baited arm compared to the low and mixed group. Together these results show that high exploratory groups are faster to forage but were relatively worse during reversal learning. This studies highlight the effects on group composition on foraging speed and routine-like behaviour.

Across a wide range of animal taxa individuals differ consistently in their behaviour, also known as animal personalities. These individual differences can be linked to fitness, affect population dynamics, and to have fundamental ecological and evolutionary implications (Conrad et al. 2011; Dingemanse et al. 2010; Denis Réale et al. 2007; Wolf 1976). However, a relatively unstudied topic is the possibility of a link between personality and cognition (A Sih and Del Giudice 2012). In humans it has long been obvious that individuals differ in their cognitive abilities and styles (Gruszka et al., 2010). With a growing interest in the cognitive abilities of non-primates, there is increasing evidence that these differences in cognition are ecologically relevant (Biro and Stamps 2008; D. Réale et al. 2010; Denis Réale et al. 2007; Andrew Sih, Bell, and Johnson 2004). The individual tendency to store and respond to information from the environment is suggested to be linked to other behavioural traits. These linked personality traits are often described in behavioural syndromes or coping styles, highly explorative animals have a proactive strategy where low explorative animals are described as being reactive. Behavioural traits that differ consistently in sticklebacks are for instance, exploration, foraging behaviour (J. W. Jolles, Manica, and Boogert 2016), aggression, speed (Jolle W Jolles et al. 2017)

and sociality (Jolle W. Jolles et al. 2015). The drive for these individual differences can be explained by, metabolic rate (Krause, Hoare, and Reeves 1998), food deprivation (Godin and Smith 1988) and the perception of predation risk (Coleman and Wilson 1998). Cognitive abilities such as learning and memory also differ consistently in animals with a proactive or a reactive strategy. Proactive animals are often faster in encountering new information, because they are faster to explore new environments (Groothuis and Carere 2005). Reactive animals are slower to explore new environments, however they sample more detailed information on a small piece of that environment (Hills et al. 2016). Proactive animals choose speed over accuracy and therefore rely less on stored information about their environment. This dilemma is also known as a trade of between exploration and exploitation and individuals differ in their tendency to prefer one over the other. Although proactive animals learn new information faster, they are by definition insensitive to updating their information about their environment. This makes them particularly bad at learning changes in their environment and reattributing a value to a certain cue. In piglets it has been shown that high resisting animals (proactive) form routine-like patterns in a T-maze and therefore perform less well in reversal learning tasks (Bolhuis et al. 2004). This has also been shown for many other animal models in personality research (Guillette et al. 2011; Sneddon 2003). However, there is also still some debate in the field as (Mamuneas et al. 2015) found that bolder sticklebacks are faster in making decisions but not less accurate.

In these studies there has been a focus on the differences in cognitive abilities of individuals, however animals are often found in social living groups. Therefore we will focus on testing groups, where individual differences are also seen in terms of social roles in the group (Flack et al. 2012; Harcourt et al. 2009; Nagy et al. 2010; S. Nakayama et al. 2013; Reebs 2000). Typically, the proactive individuals lead and the reactive individuals follow (Beauchamp 2015; Harcourt et al. 2009; Kurvers et al. 2009; S. Nakayama et al. 2013). Social feedback is an important factor in modifying the social roles, where proactive individuals are often less responsive to their partners behaviour and reactive individuals are more flexible in their following behaviour (Jolle Wolter Jolles, Aaron Taylor, and Manica 2016; Shinnosuke Nakayama et al. 2012; Shinnosuke Nakayama, Johnstone, and Manica 2012). Consistent individual differences do not only effect leadership as described above (Harcourt et al. 2009; Kurvers et al. 2009; Pettit et al. 2015; Ward et al. 2004), but can also have other structural group effects for instance on, social network structure (Aplin et al. 2013), collective dynamics (Farine et al. 2017; Jolle W. Jolles et al. 2015), and group performance (Dyer et al. 2009; Laskowski, Montiglio, and Pruitt 2016; Pruitt and Riechert 2011). Living in groups provides safety from predators, cause earlier predator detection and greater foraging success (Couzin et al. 2002). By living in social groups animals can pool their competences, by combining knowledge that individuals learned independently to create collective intelligence also known as “wisdom of the crowds” (Kao et al. 2014). Pooling of competence can lead to greater foraging success, more mating opportunities and better predator detection (Dyer et al. 2009; Pruitt and Riechert 2011). Since individuals differ in their cognitive abilities and these differences are associated to their personalities, group learning might be most efficient when a group is composed of a mixture of personalities.

This study is designed to get a better understanding of the effects of group composition on group performance in a foraging task. Three-spined sticklebacks were used to study group

composition effects and group learning, as they are a social species (Bell and Sih 2007; Harcourt et al. 2009; Jolle W. Jolles et al. 2014; Mike M. Webster and Ward 2011) that have a strong tendency to shoal. The inter-individual differences are robust and can be measured individually by exploration levels (Jolle Wolter Jolles, Aaron Taylor, and Manica 2016). Individual sticklebacks can learn the location of a food patch in an experimental setting relatively fast (Mamuneas et al. 2015) and individual and group foraging are affected by group composition (Jolle W Jolles et al. 2017).

We will test the effects of group exploration levels on group learning and reversal learning. Therefore we screened individual three-spined sticklebacks (*Gasterosteus aculeatus)* for exploration and subsequently assigned them to low, mixed or high exploration groups. These groups were then subjected to a Y-maze learning task, where they learned the location of a food patch. The baited arm was switched after 12 initial learning trials to study reversal learning. We expect groups with a high amount of high exploratory individuals to learn faster, however they form routine-like patterns which would make them worse at reversal learning. Groups with a high amount of low exploratory animals might learn slower, but are expected to be more flexible in reversal learning. In a mixed exploration group we expect competence to be pooled making the group both fast and flexible in learning the location of a food patch.

METHODS

Animal Housing

Three-spined sticklebacks (*Gasterosteus aculeatus*) were caught from lake Constance with a sweep net (n=96). The fish were socially housed with 64 individuals, in a glass holding aquarium of 90 x 50 cm and 21 cm with artificial plants and constant fresh water flow (T=14±1˚C), and fed frozen bloodworms (*chironomid larvae*) ad libitum once a day. All animals were treated for parasites and were roughly the same age and size, since they were taken from a single population to minimize population-specific genetic effects that may influence personality (Bell 2005). Although the exact age of the fish could not be determined, all caught individuals were juveniles and only varied in age with a couple of weeks. The light-dark schedule was 8:16, with lights on at 8:00 pm. These conditions did not allow for any sex differences to occur and therefore we did not sex the animals before the experiments (Borg et al. 2004). Three days before the experiments animals were transferred to individual housing compartments (18,5 x 9,5 cm and 16 cm high) in perspex tanks. In the individual housing tanks the sticklebacks were able to see at least two conspecific through a perforated plastic wall that allowed for passage of any visual or chemical cues. The tanks had a steady flow of lake water running through them and each individual compartment contained an artificial plant with a diameter of 4 cm made from green plastic and sand. Food was rationed to one bloodworm per day to standardize hunger levels. The fish had not been used in previous experiments.

Individual Exploration

The exploration tendency was assessed by measuring the time spent out of cover in an open environment. The fish were tested individually two times with one day in between for consistency in behaviour. The experimental arena (75 x 50cm and 8 cm high) contained two patches of two plastic plants (d=6 cm) as cover, located 15cm from the wall in the middle of the tank. We used the time spent out of cover as a measurement for the amount of individual

exploration. This test reflects an ecologically relevant measurement where fish can either rest in a safe place or explore a potentially risky area for reward. Sticklebacks usually prefer to stay under cover, but even in the absence of food or other rewards they make regular trips in the open area (Harcourt et al. 2009; Jolle W. Jolles et al. 2014; S. Nakayama et al. 2013). The individual tendency to spent time out of cover differs consistently between individuals and is highly correlated to other boldness measurements (Jolle W. Jolles et al. 2015). To minimize disturbances from outside of the tank, the testing tanks were placed in a white tent. A camera was fixed above each tank to record behaviour. The experiment lasted for 10 minutes and the animals were placed in the a see-through start box where they habituated for 1 minute before the start of trial.

Group composition

After acquiring the behavioural types of the individual fish we created specific group composition to study group learning. The average of the two individual tests was used to determine the exploration rank for all animals. The distribution of exploration ranks was then divided in 8 subsets of data, from the subsets we randomly assigned individuals to their allocated group.

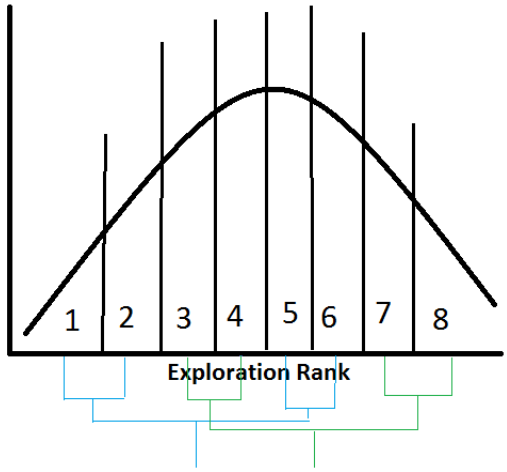

Fig. 1. Schematic overview of the allocation of fish to their groups according to exploration rank. The blue and green lines represent the allocation of fish from the mixed groups, where two fish from the lowest exploration subgroups are combined with the two least highly explorative subgroups or reversed.

The low exploration groups consisted of one fish from each of the 4 lowest exploration subsets, for the high exploration groups these are the 4 highest exploration subsets (figure 1). The mixed groups consisted of fish, from either the 2 lowest exploration subsets and the 2 relatively less high exploration subsets or two fish from the most high exploration subset and 2 from the least low explorative groups (see blue and green lines in figure 1). In total, we tested 24 groups, containing 4 individuals each, 8 low exploration, 8 mixed and 8 high exploration groups. All the fish in the group were tagged with a small coloured plastic tag on the second dorsal spine (M. M. Webster and Laland 2009) for individual identification. They were randomly assigned the colour: blue, green, grey or yellow and treated for potential fungus infection for 24 hours, 1 day prior to the start of the learning trials.

Learning Experiments

Before starting the learning trials the groups were accustomed to handling, their group mates and eating still worms in the experimental tank during a 30 minute trial in an empty tank with 8 bloodworms scattered through the tank. The order of testing and the tank number was randomized between testing days, allowing for a 2h break between trials where the fish were in placed back into their individual housing compartments. The initial learning phase was completed in 4 days with 3 trials per day, the reversal learning took 2 days with 4 trials per day. Before the start of the experiment the animals were habituated in a small see through cylinder (start box) for 30 seconds in the experimental arena. The start boxes were manually lifted and that marked the start of the experiment.

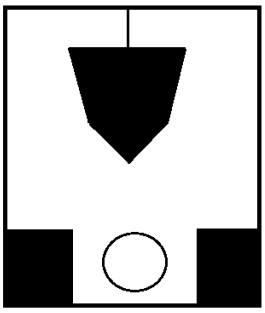

Fig. 1b. Schematic overview of the experimental arena for the learning trials. Y-maze with visual cues on the walls and the start box at the beginning of the tank.

The experimental arena (75cm x 50cm and 8cm high) consisted of a Y-maze with two arms containing visual cues to aid learning (Figure 1b, Figure 10 in supplementary data). The food patch consisted of 8 bloodworms and was not visible at the location where the fish decide to go into one arm or the other. The duration of the first learning trial was 10 minutes and the other 19 trials took 5 minutes. During reversal learning the location of the food patch was switched to the other arm, while the visual cues on the walls remained the same. The videos were recorded using raspberry pi camera`s at 24 frames per second. They videos were scored manually on the following measurements, the moment the start box was lifted, the entry of the correct/incorrect arm and timing of individual food intake. With these measurements we calculated the latency for the first individual to enter the correct/incorrect arm and the individual food intake over trials with known identities and exploration score.

Data analysis

The exploration ranks were normally distributed and subsequently tested for differences with a one-way ANOVA and for consistency with Spearman and Pearson correlation test. They were also tested with a Mixed Model for a robust analysis. The proportion of time spent out of cover was not normally distributed (Trial 1: W=0,88; trial 2: W=0,91), therefore the data was transformed logarithmically (Trial 1: W=0,93; trial 2: W=0,91). Since the data was not normally distributed the Kruskal Wallis test was used to test multiple samples that originate from the same distribution. The average differences in exploration between the different groups is χ^2=20,48 with 2 degrees of freedom, p<0,01. The variance of exploration between the groups was tested by the Levene test $F_{2,21}$ = 112,93 p<0,01. This indicates that, the variance between the groups was large, this was due to the high variance in exploration in the mixed group. The

low and high exploration groups did not differ in terms of variance (VarTest $F_{7,7}$ =0,52 p=0,408). The learning trials were scored on both accuracy of the first entry of the arm as well as the latency to reach the correct arm. The latency to enter the correct arm was not normally distributed (*W*=0,588; p=0,000, Shapiro Wilk). Further analysis on the learning experiments were done with a univariate general linear model and a posthoc Tukey test. The depended variable was either the latency to the correct arm or the correctness of the first arm entry. The group composition was the fixed factor and group ID was a random factor. The initial learning (trial 1/12) and reversal learning (trial 13/20) are tested separately in these models. Values are considered significant if p<0,05 shown with standard error. Analysis were done using R-studio and IBM SPSS Statistics Data Editor.

During the last three days of the experiment 11 out of the 96 fish died due to severe fungus infection. The groups with the missing fish were still tested with the remaining three group mates, there were never groups with less than 3 fish. On four occasions no video was recorded of the trial, on three other occasion no food was provided during the trial. These factors were not taken into account during the analysis of the data, but are well documented for future analysis.

RESULTS

During the individual exploration task fish spent 61,7% ± 3.0 stderror of their time out of cover with a large range of 0%-99%. On the second test the overall time spent out of cover was decreased non-significantly (p>0,5) to an average of 53,2%± 3,2 stderror and with a range of 0%-96%. The exploration ranks that were extracted from the individual exploration tests were highly correlated between the two testing days (*r*s=0,69 Spearman), using more robust analysis also showed a high consistency between testing days (*R*=0,66, 95% confidence interval: 0,52-072).

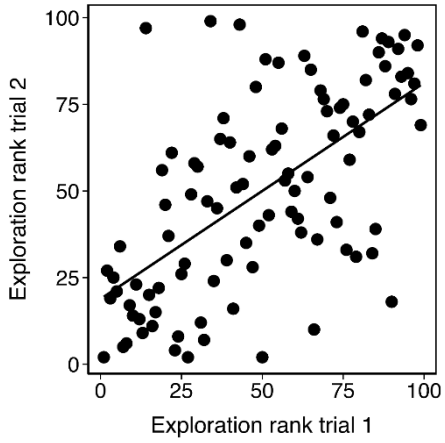

Fig. 2. Correlation between the first and second exploration rank score.

On average the groups became faster at reaching an arm (*r*=-0,391, p<0,05) and also at reaching the correct arm (*r*=-0,282, p<0,05), during the initial learning phase. The latency to the correct arm was increased significantly when the baited arm was switched for all groups (comparing trial 12 with trial 13, T-test; p<0,05) (see figure 3). Visual inspection of the learning trials showed that most groups perform above chance level in choosing the correct arm after 8 trials ,this was indeed confirmed by comparing the last trial of the initial learning phase with the first trial (Trial 1 vs trial 12 T-test, P<0,05). On average the groups also became significantly

worse in choosing the first correct arm after reversing the baited arm (see figure 4). In the last reversal learning trial, all groups re-learned the new arm since they were significantly faster compared to the first reversal learning trial (Trial 12 vs 13 T-test, p<0,05), however they were still not as fast as they were compared to the last trial of the initial learning phase (Trial 12 vs 20 T-test, p<0,05).

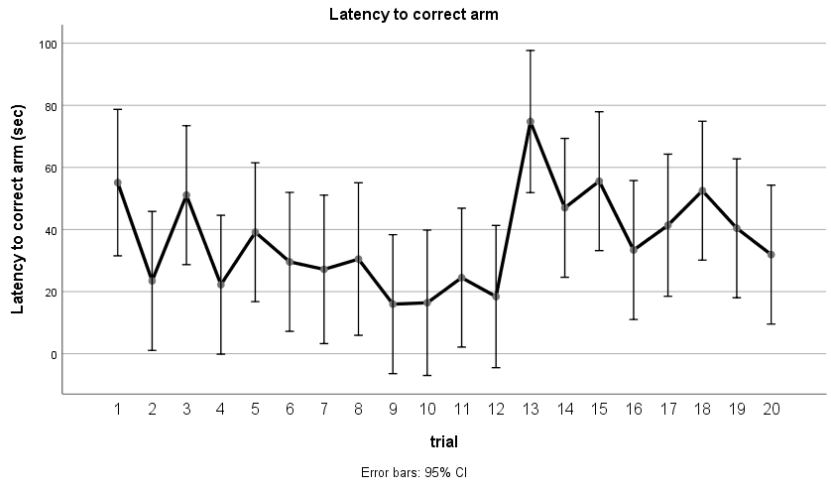

Fig. 3. Latency to enter correct arm for all groups (n=24). The averages are plotted with the 95% confidence interval. Trial 13 is the first trial for the reversal learning phase and the latency to the correct arm is significantly increased compared to trial 12 (last trial from the initial learning phase). The last trial for the reversal learning, trial 20, is significantly lower than trial 13, but higher then trial 12.

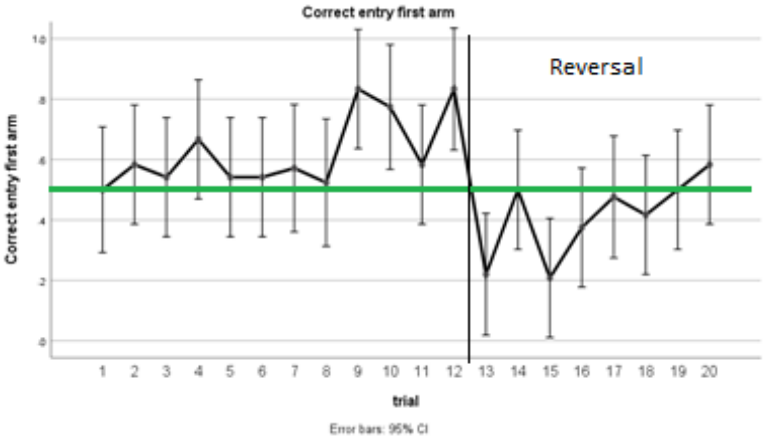

Fig 4. First entry of the correct arm of all groups (n=24) average and 95% confidence interval. The green line indicates the chance level. At trial number 13 the baited arm is switched (reversal learning). Trial 12 differs significantly from trial 13 (p<0,05).

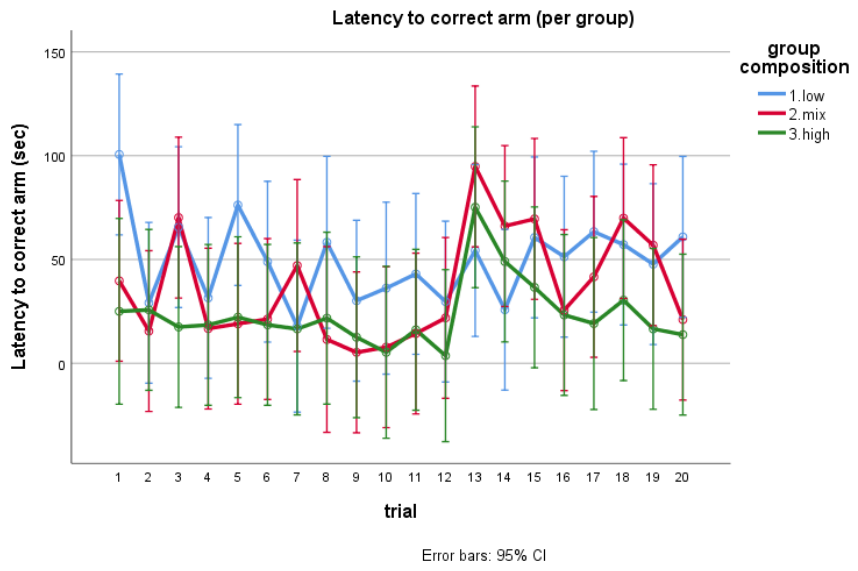

Fig. 5. Latency to the correct arm plotted for the different group compositions (n=8). Trial 1/12 are part of the initial learning phase and trial 13/20 are part of the reversal learning phase.

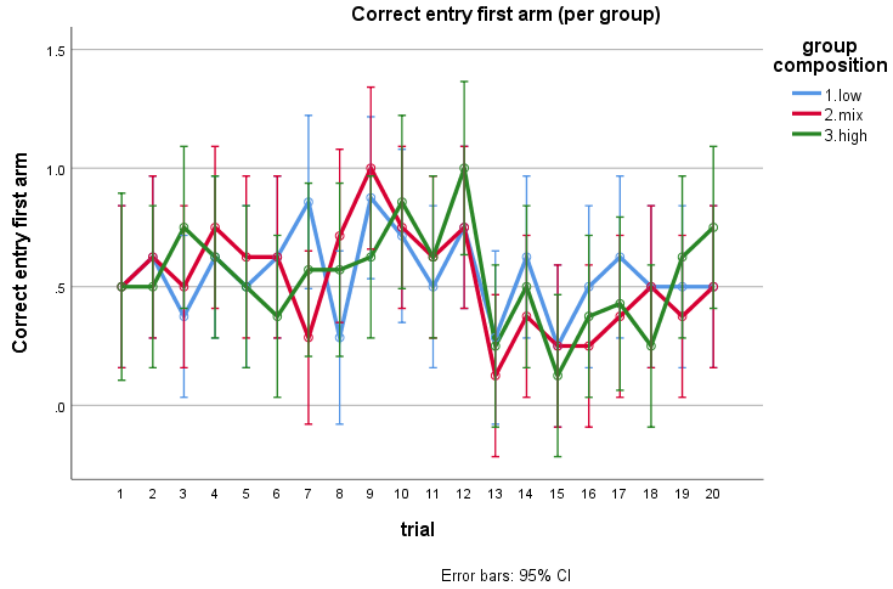

Fig. 6. First entry of the correct arm per group composition (n=8), plotted are the averages per group composition and 95% confidence interval.

Looking in more detail at the potential effects of group composition, we found that during the initial learning phase (first 12 trials) group composition significantly explained the data for 61,8% and 53% respectively in the general linear model. Post-hoc analyses showed that, the low exploration groups were significantly slower in reaching the correct arm compared to the mixed and high exploration groups ($p<0,002$), however the mixed group and the high exploration group did not differ (Posthoc Tukey $p=0,517$). Group composition did not predict the correctness of the first arm the fish entered ($p>0,05$). For all the models we ran no interaction with group composition and trial was found. When the baited arm was switched (trial 12 vs 13), high exploratory groups showed a significant bigger increase in their latency to

find the correct arm compared to the low exploratory groups. It took the high exploratory groups on average 20,5x longer to find the baited arm when we compare trial 12 with trial 13, for the low and mixed groups this was an increase of 1,8x and 4,3x. During reversal learning (trial 13/20), group composition no longer predicted the latency to an arm and in a model investigating the latency to the correct arm it now only predicts 36,5% of the data.
The number of prey items eaten was equally distributed between all the members of the group over all the trials. There was no effect of exploration rank within the group between the different group compositions (General linear model p>0,05, figure 7).

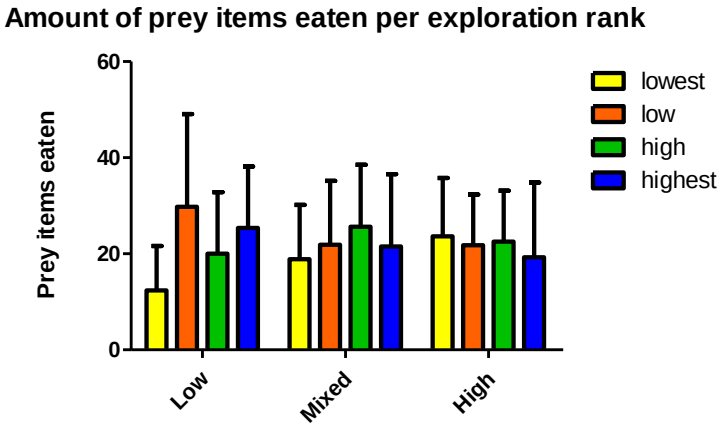

Fig. 7. Overview of the amount of prey items eaten during the initial learning phase, averages with standard deviation. Within the groups individuals are ranked as the least or most exploratory, these are then compared for the different group compositions.

DISCUSSION

By testing fish on exploration and assigning them to specific groups we aimed to uncover the effects of group composition on group learning in a foraging context. We tested groups in a Y-maze with one baited arm, after 12 trials we switched the baited arm to study reversal learning. The exploration level of the group had an effect on the latency to enter an arm and also the latency to enter the correct arm. Almost all groups learned to associate the baited arm with food after ± 8 trials, there were no significant differences in doing so between the groups. When the baited arm was reversed high exploration groups took on average 20,5x longer to reach the new baited arm, this increase is significantly different from the low and mixed groups. This implicates that even though high exploratory groups are faster to find food they struggle much more compared to the other groups when the environment is changed. Suggesting that high exploratory groups form routine-like patterns in a foraging context, where low exploratory groups keep sampling information.
Looking into the success off learning and the effects of group composition, most groups learned to associate a certain arm with food after 8 trials as most of the groups by then performed above chance level. This was significantly decreased when the baited arm was switched during reversal learning, further indicating that the 12 initial learning trials were sufficient to establish learning in all groups. Even though, all groups learned to associate the baited arm with food, no effect was found on group composition in doing so. During the initial learning trials high exploration groups were faster at reaching the correct arm compared to

the low groups, but significantly faster than the mixed groups. One possible explanation for this, is that highly exploratory animals are more motivated to seek out reward/food and thus swim faster. The increased motivation to seek out food in bold animals may arise from growth-mortality trade-offs (Biro and Stamps 2008), that links energetics to personality research (Careau and Garland 2012). Individuals with high growth rates are adapted to their energy needs in terms of physiology and behaviour, they tend to take more risk (i.e. bolder) and have a higher food intake. Indeed food intake is positively correlated with boldness in sticklebacks. A similar set-up to ours is used to test for boldness/exploration effects on food intake (Jolle Wolter Jolles, Aaron Taylor, and Manica 2016). Based on this research we expected the high exploratory animals in the mixed group to have a higher food intake. However, we found that in a mixed group the high exploratory animals did not eat more compared to the low exploratory animals. Perhaps this is due to the perceived risk, or because the fish are not in their resting state as in (J. W. Jolles, Manica, and Boogert 2016). The Y-maze used was relatively small and the lifting of the start box was not automated which made the fish anxious to reach the other side of the tank where the food patch was located. This might have influenced the learning rate of the correct location of the food patch, it would be better to have a circular arena where the start box lift is automated to reduce stress. On the walls of the maze we used horizontal and vertical bars as visual learning aids to differ between the two arms (Odling-Smee and Braithwaite 2003; Boogert et al., 2017 unpublished). It is not well known what cues sticklebacks use for learning, however this was beyond the scope of our experiment and so we used previously known cues.

The equal distribution of food does suggest that all group members received the same learning reinforcement. It is most likely that the low exploratory animals follow the faster high exploratory animals when foraging. This is also evident from the foraging data, where there are no significant differences in food intake in the mixed group between the low and high exploratory animals. The equal distribution of food means that all the individuals within the group received the same reward and learning reinforcement.

In terms of reversal learning we found a trend where it took the high exploratory and mixed group longer to find the correct arm compared to the low exploratory groups. The high exploratory groups took 20,5x longer to find the baited after it was switched. This a clear sign of a routine-like pattern, especially if you keep in mind that high and mixed group were faster during the initial learning. The low exploratory groups had a similar latency to find the correct arm during the initial learning phase as well as during the reversal learning phase. This is in line with our hypothesis that low exploratory groups kept sampling their environment much more making them slower but more flexible in learning new cues. We also observed high exploratory groups that never entered the correct arm after the first reversal learning trial, this clearly suggest routine-like behaviour. It would be interesting to see whether all high exploratory groups members showed this routine-like behaviour or if they followed a leader that showed routine-like behaviour. In the mixed groups we didn`t observe these routine-like patterns which suggest that it is not just the high exploratory leader that causes routine formation on a group level. It could be that the all high exploratory group reinforce each other to make the wrong decision. This also suggests that mixed groups perform better since they are fast to reach the correct arm and do not take much more time to find the correct arm when the food patch is switched, indicating that they are flexible in updating their information.

We will now discuss the group formation process based on the individual exploration levels. The individual exploration levels were measured twice in an empty tank with two patches of cover, time spend out of cover is taken as a measurement for exploration. We found that more animals were highly exploratory and therefore the data was skewed. This could be due to the natural habitat of the three-spined sticklebacks, since all the fish were taken from lake Constance it is possible that these fish don't use plant cover as often as for instance stream sticklebacks (Berner et al. 2008; D. Moser, Frey, and Berner 2016; Dario Moser, Roesti, and Berner 2012). However, the inter-individual differences in exploration are still valuable in lake species since they still perceive open areas as more risky.

In order to study individual difference we used coloured tags, this procedure resulted in the death of 11% of the individuals, despite the treatment for anti-fungus before and after the tagging procedure. Previous studies using the same method have had lower mortality rates (M. M. Webster and Laland 2009), this could be because we used untreated water from lake Constance. In the future the mortality rate could be decreased by using UV-filtered water to kill possible bacteria and viruses. The relatively high mortality rate consequently caused some of the groups to continue testing with only three group mates, this could possibly influence the data and therefore it should be taken into account as a factor in further analysis.

In the future we would like to track the individuals using their coloured tags, in order to establish leadership, group cohesion and social information transfer. The measurements we scored in this study are not precise enough to describe the point of decision making and which individual in the group is involved in decision making. The data we scored for entering an arm is further down in the maze after the point of decision making, this could be improved by tracking. Studying leadership will give us insight on the relation between exploration levels and previous information about the environment to shoal positions. It will also be interesting to see if the leaders are also the individuals that feed first upon finding the food patch and how the information about the food patch is transferred among the group members. Group cohesion is believed to not be influenced by personality and speed is more important for group cohesion (Jolle W Jolles et al. 2017). By comparing the mixed groups with the low and high exploratory groups we could see if there is a difference in swimming speed in the mixed group effect cohesion of the group. We could also study social information transfer by not only scoring food intake but, also if sticklebacks observed others feeding and how many other group mates were present in the baited arm during feeding or observing. Future studies are also needed to understand the individual learning rate and routine-like behaviour related to exploration levels.

To conclude, we found that exploration levels of individuals within the group had an effect on the latency to find a food patch. High exploratory and mixed groups were faster at reaching the baited arm compared to low exploratory groups. However, high exploratory groups were worse during reversal learning, meanwhile the low exploratory groups did not differ in their latency to finding the baited arm. This suggests that high exploratory groups form routine-like patterns, while low exploratory groups keep sampling their environment throughout the experiment. The mixed groups seem to be pooling the competence of both strategies as they are both fast and flexible in learning the location of the food patch. This study highlights the importance of having a diverse individuals within a groups to optimize group performance. For

wild groups of sticklebacks this would implicate trading off speed against a wide variety of personalities will ultimately benefit the entire group.

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SUPPLEMENTARY DATA

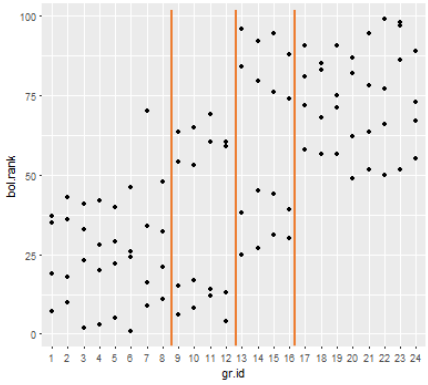

Fig. 8. Boldness rank per group with 4 individuals per group. Group 1- 8 are considered low exploratory, 9-16 mixed with either the lowest with the least high exploratory fish or the other way around, 17-24 are high exploratory groups.

Fig. 9. Picture taken from the outside of the tank, the baited arm is on the left side in this case and the visual cues are present on the walls of the maze. The fish are waiting in the start box for the beginning of the trial.