



Original Article

Collective decision making in guppies: a cross-population comparison study in the wild

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Received 8 August 2016; revised 1 February 2017; editorial decision 25 February 2017; accepted 15 March 2017; Advance Access publication 7 April 2017.

Collective cognition has received much attention in recent years but most of the empirical work has focused on comparing individuals and groups within single populations, thereby not addressing evolutionary origins of collective cognition. Here, we investigated collective cognition in multiple populations that are subject to different levels of predation. Guppies (*Poecilia reticulata*) were given a simultaneous choice between an edible and a nonedible stimulus. We found evidence for an improvement in decision accuracy when in groups but only in low-predation guppies. This performance increase was due to a combination of increased private sampling behavior when in groups (compared to being alone) and social information use. In contrast, high-predation fish did not sample more when in groups, nor used social information; hence did not improve decision-accuracy when in groups. The improvement of groups in foraging accuracy in low but not in high-predation sites, suggests that these populations differ in their trade-off between attention dedicated to food and predators. In high-predation sites, investing time in predator detection is more crucial than in low-predation sites, thereby possibly conflicting with food detection. Our results highlight the importance of considering the effects of ecological gradients on collective cognition.

Key words: collective cognition, guppy, *Poecilia reticulata*, social information use.

INTRODUCTION

Sociality confers many advantages to animals, such as better anti-predator defense or food detection (Krause and Ruxton 2002). Many of these advantages result from collective cognition, which is the ability of members of groups to make better decisions than single individuals (Krause et al. 2010). Animals often gain advantage from cues that are inadvertently displayed by their conspecifics, using this social information to complement their own information to make better decisions (Danchin et al. 2004). For example, rats infer from their congeners' breath whether some food is safe or not

to consume (Galef 1991), whereas starlings observe the foraging success of their flock mates to assess the quality of a food patch (Templeton and Giraldeau 1995). Social information is also used by animals to make collective decisions. Often, these decisions may be based on quorum thresholds. For instance shoals of stickleback (*Gasterosteus aculeatus*) use quorum thresholds to evaluate predation risk (Ward et al. 2008) or to locate foraging patches (Ward et al. 2012). Similarly, ant colonies that are forced to emigrate from their nest are able to choose the best available new nest by accelerating the recruitment process once a threshold number of ants have made a decision in favor of a particular location (Pratt et al. 2002; Sumpter and Pratt 2009). It was also shown in fish shoals that the speed and the accuracy of decisions increased with group size (Ward et al. 2011).

One important selection pressure affecting the use of social information is thought to be predation risk (Elgar 1989; Devereux

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et al. 2006). For example, experimentally increasing the perceived risk of predation in the lab resulted in an increased reliance on social information in minnows (*Phoxinus phoxinus*) due to increased cost of gathering private information (Webster and Laland 2008). In sticklebacks, 9-spined sticklebacks rely much more on social information than 3-spined sticklebacks and this is thought to be due to their smaller body armor (as compared to 9-spined sticklebacks), making it riskier for them to collect private information (Coolen et al. 2003; van Bergen et al. 2004; Coolen et al. 2005). In Barnacle geese, a reduction in social information use coincided with reduced hunting (Kurvers et al. 2014). Furthermore, predation risk has been shown to influence social structure of animal groups (Kelley et al. 2011), possibly affecting information transfer and social learning. However, a largely unresolved question is how individuals from populations under different predation regimes in the wild differ in their use of private versus social information.

Many fish species feed on objects falling into the water and individuals have to respond quickly to a stimulus and consume it before others do (Krause 1993). For example, carotenoid pigments have been shown to confer direct health benefits to guppies (Kolluru et al. 2006) and they are used in courtship displays by males (Kodric-Brown 1989). They cannot be synthesized by guppies and must be obtained through their diet (Fox 1976), mostly by consuming orange and red fruits that fall in the water. Both males and females are highly attracted by these red fruits (Rodd et al. 2002). However, the streambed usually contains many other reddish objects including pebbles that are nonedible and fish will often approach objects that they cannot consume thereby wasting energy, missing simultaneously occurring and genuine feeding opportunities, and exposing themselves to predation by breaking their crypsis through movement (Ioannou and Krause 2009; Hall et al. 2013).

In many natural situations, timing matters. For example, detecting and responding to a predator earlier increases the chance of survival, because predators focus on individuals that react more slowly (Kenward 1978; van der Post et al. 2013). Similarly, in a foraging context, being part of a group implies competing with other members when the food is limited and a rapid response to opportunities can increase food intake. For example, one fish might benefit from social information about a fallen object by watching how the others react to it but a delayed response may mean a missed opportunity. Researchers have previously looked at single populations in the context of decision accuracy (Sumpter et al. 2008; Ward et al. 2008; Ward et al. 2012) and there is evidence for decision accuracy to improve with group size (Couzin 2009; Krause et al. 2010; Clément et al. 2013; Wolf et al. 2013; but see Kao and Couzin 2014) and for social information use to be selected in risky environments (Webster and Laland 2008) but these 2 components have not been integrated yet.

Using the comparative approach to investigate groups of free-ranging guppies, *Poecilia reticulata*, from 4 different populations facing different predation regimes, we studied the effects of the presence of conspecifics and predation level on decision accuracy by presenting fish simultaneously with an edible and a (similar looking) nonedible item. We quantified how frequently the edible and the nonedible stimuli were targeted as a measure of decision accuracy. Furthermore, as the accuracy of the decision could be affected by the activity of the individuals, we studied how the presence of conspecifics and the predation level affected sampling activity and how sampling activity, in turn, affected decision accuracy. We predicted that decision accuracy is higher for individuals in groups than for singletons and, if so, that this performance increase in low-predation populations is primarily caused by an increase

in private sampling whereas in high-predation sites it should be brought about by greater use of social information.

METHODS

Experimental setup

The study took place in the Turure River (lower: 10°39'27"N, 61°9'48"W; upper: 10°41'7"N, 61°10'23"W) and the Aripo River (lower: 10°39'1"N, 61°13'26"W; upper: 10°40'55"N, 61°13'51"W) in Trinidad (March 2013, 2014, and 2015). These rivers consist of interconnected pools inhabited by different-sized guppy populations (*Poecilia reticulata*). Both streams are known to have a sharp gradient in predation pressure: In the lower sections (below the main falls) characids and cichlids are present, which heavily predate on guppies. These predators are absent in the upper sections (above the main falls) (Magurran 2005). This provides a unique opportunity to use a natural gradient in predation pressure to investigate its effect on collective cognition. We sampled populations from below and above the main falls in both rivers. Additionally, it has to be noted that during the whole duration of the present study and on numerous previous occasions in the study area, no aerial predator were observed. Seghers (1974) also documented geographic variation regarding the presence of aerial predators in some areas of Trinidad and their absence in other areas.

We made an edible stimulus and a nonedible stimulus out of red material. The edible stimulus was a piece of red bell pepper and the nonedible stimulus was cut out of red plastic. Both stimuli had the same shape (9 × 5 × 2 mm) and each was fixed to a weighted monofilament line (40 cm long, ø 0.2 mm) attached to the end of a wooden rod, 20 cm apart from each other. We first conducted pilot trials to verify that both stimuli were effective with fish in the wild when presented in isolation (mean ± SE number of approaches toward the edible stimulus during the whole 2 min trials: 4.1 ± 0.5 (*N* = 30), toward the nonedible stimulus: 2.6 ± 0.4 (*N* = 37). An approach was defined as the focal individual moving toward the stimulus within one body length from it.

In both low- and high-predation sites, we walked transects along the river and opportunistically searched for singletons and groups of guppies. Group sizes (median (full range, number of trials)) were 3 (1–40, *N* = 186) for the upper Turure, 6 (1–50, *N* = 165) for the lower Turure, 8 (1–50, *N* = 120) for the upper Aripo, and 8 (1–70, *N* = 136) for the lower Aripo. Upon encountering a singleton or a group, we targeted them with the choice experiment. In case of a group, we counted the number of guppies present and to avoid pseudoreplication, we randomly selected one as focal individual. The focal individual was not marked because marking would have required catching all individuals, which would have disrupted the group dynamics, in addition to being extremely time consuming. Furthermore, pilot trials had shown that the fish are not too mobile and that it is possible to follow a fish individually, even within a group, for several minutes. However in a few trials, the focal individual was lost and these trials were discarded. Both stimuli were then slowly and simultaneously lowered into the water approximately equidistant from the focal individual (and whenever possible also equidistant from the whole group). Trials lasted 2 min following the introduction of the stimuli, giving the fish sufficient time to inspect both stimuli (although our main results did not change when considering shorter time periods [down to 30 s]). We scored the number of approaches made by the focal individual toward the edible and the nonedible stimuli. In total, 607 trials were conducted, testing fish in group sizes ranging from 1 to 72 (mean group size = 6.2). Each

trial was carried out in a different location along both streams and it is thus highly unlikely that the same groups or the same individuals were tested twice. Note that the number of groups encountered was higher than the number of singletons. This was taken into account and the significance analysis support the results.

Analysis

For each randomly selected individual, we quantified every approach toward each stimulus and we investigated the effect of the presence of conspecifics and of the predation level on sampling activity and on decision accuracy. We defined sampling activity as the total number of approaches by the focal individual toward either stimulus within the 2 minutes following the lowering of the stimulus in the water. We defined decision accuracy as the ratio between the number of approaches by the focal individual toward the edible stimulus and the total number of approaches by the focal individual. As some fish did not approach any stimulus during the whole trial (129 out of 607 trials in total), including them in our analysis would have biased decision accuracy toward 50%, whereas no decision was made in these cases. We therefore considered only the trials where there was at least one approach.

We first looked at the ability of singletons to distinguish between the 2 stimuli at their first approach using a binomial test. We then looked at the accuracy of the first approach using accuracy as response variable in a generalized linear model with group size and predation level as explanatory variables. We used binomial errors and a logit-link function because the response variable was binary (with 0 indicating that the first approach was made toward the nonedible stimulus and 1 indicating that the first approach was made toward the edible stimulus). This analysis was performed using R version 3.2.2 (R Development Core Team 2015).

We reasoned that the importance animals give to social information could be affected by whether they found an edible stimulus in the first approach. In these cases, because they get enough relevant private information on their own, they could in principle ignore more what the other group members are doing and this effect could vary between predation levels. We thus analyzed the data separately, according to the first decision they made (i.e., correct or incorrect) and investigated their ability to use social information to change or confirm their initial decision depending on predation level. As fish from high-predation populations showed lower activity, we did not compare the accuracy of fish from the 2 populations directly. Instead, we conducted our analysis of decision accuracy of fish from low predation and from high-predation populations separately. For each predation level, we then separated the trials in either singleton or group trials. We obtained similar results when analyzing only subsequent approaches (i.e., excluding the first one).

All statistical tests to compare the differences between each 2 distributions were conducted by using a standard permutation test for the mean and thus required no assumptions about the type of distributions (see Good 2005; Edgington and Onghena 2007; Bonnin et al. 2014 for more details regarding this method). Specifically, the 2 datasets were put together and, for 100 000 times, we randomly separated the joint dataset into 2 new distributions. We obtained, for each time, the difference between the means of the 2 groups and computed the P -value as the proportion of times in which this difference was higher than for the original datasets. The level of significance was chosen at $P = 0.05$. This analysis was performed using Matlab (The Mathworks 2013).

Ethics statement

This research was performed in accordance with the laws, guidelines and ethical standards of the country in which they were performed (Trinidad).

RESULTS

The proportion of singletons first approaching the edible stimulus was not significantly different from 0.5 ($N = 87$, $P = 0.284$, Figure 1). However, group size had a significant positive effect on the probability that the first approach is made toward the edible stimulus (glm: $N = 477$, $X^2 = 11.53$, $df = 1$, $P < 0.001$; Figure 1).

After making a first wrong approach, we found that individuals in the low-predation sites were significantly more active ($P = 0.004$; Figure 2a) and significantly more accurate (i.e., more approaches toward the edible stimulus, $P < 0.001$; Figure 2a) when part of a group ($N = 64$) than when alone ($N = 30$). However, for individuals in the high-predation sites, we found no significant difference in activity ($P = 0.196$; Figure 2b) and in accuracy ($P = 0.092$; Figure 2b) between individuals alone ($N = 19$) and those that are part of a group ($N = 67$).

After making a first correct approach, we found that individuals in the low-predation sites were significantly more accurate (i.e., more approaches toward the edible stimulus, $P = 0.009$; Figure 2c) when part of a group ($N = 118$) than when alone ($N = 26$). However, they did not sample more in groups than as singletons ($P = 0.205$; Figure 2c). For focal individuals in the high-predation sites, we found no significant difference in activity ($P = 0.338$; Figure 2d) and in accuracy ($P = 0.356$; Figure 2d) between individuals alone ($N = 12$) and those part of a group ($N = 115$).

DISCUSSION

We found that only low-predation guppies were able to improve their decision accuracy after making an incorrect first choice. As

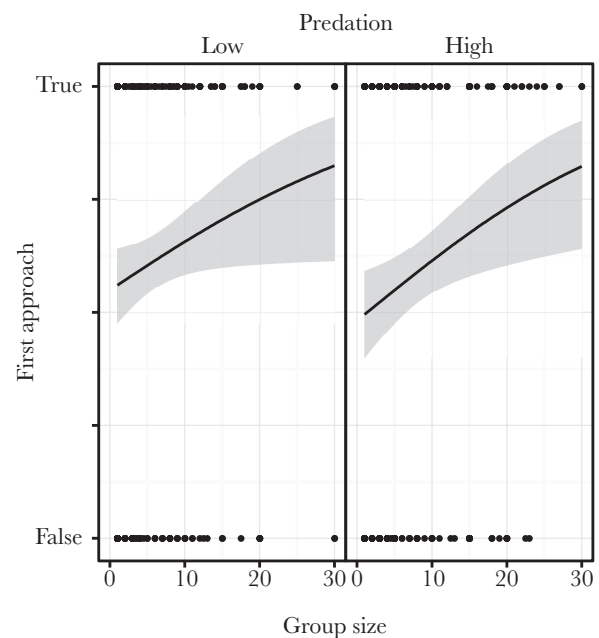


Figure 1

The accuracy of the first approach significantly increased with group size, both in high and low-predation levels. Logistic regression line is shown with 95% confidence interval (shaded area).

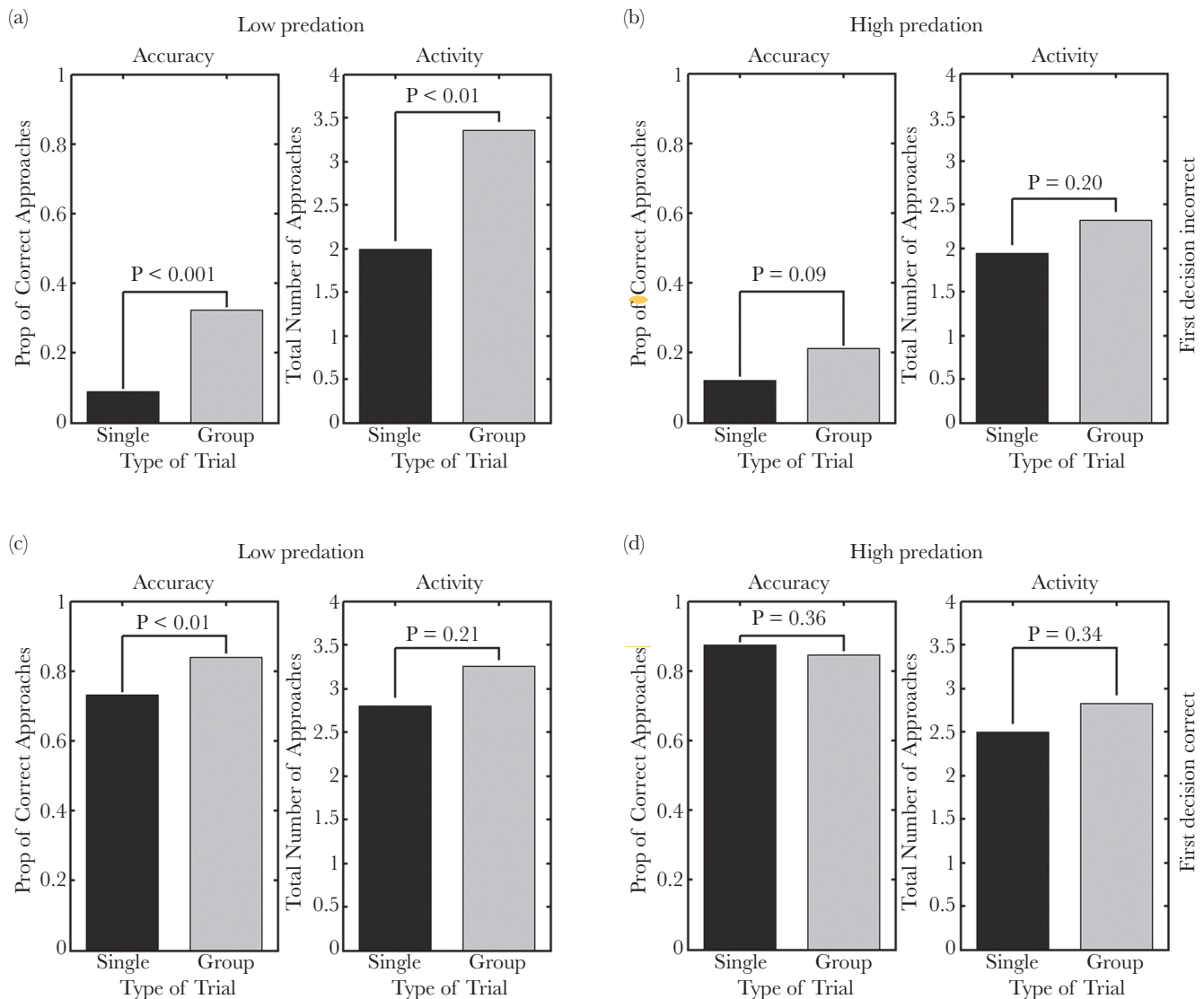


Figure 2

(a) After making an incorrect initial approach, we found that focal individuals in low-predation sites were significantly more active and accurate (i.e., more approaches toward the edible stimulus) when part of a group than when alone. (b) However, for focal individuals in the high-predation sites, we found no significant difference in activity or accuracy between individuals alone and those that are part of a group. (c) After making a correct initial approach, we found that focal individuals in the low-predation sites were significantly more accurate (i.e., more approaches toward the edible stimulus) when part of a group than when alone. However, they were not significantly more active in groups than when alone. (d) For individuals in the high-predation sites, we found no significant difference in activity or accuracy between individuals alone and those that are part of a group.

expected, this performance increase was partly due to increased sampling behavior when in groups (compared to being alone) but there was also evidence for the use of social information. In contrast, we found no evidence in high-predation fish to improve their decision-accuracy when in groups and therefore no indication of social information use.

Our results contrast with previous studies that showed that social information use is higher in species that are more vulnerable to predation. Nine-spine sticklebacks (*Pungitius pungitius*), which are more vulnerable to predators than 3-spine sticklebacks (*Gasterosteus aculeatus*), rely more on the presence and feeding rate of conspecifics and heterospecifics to decide on which food patch to approach (Coolen et al. 2005). We found no evidence for high-predation guppies to use social information whereas low-predation guppies did. The presence of predators might influence the trade-off between the use

of private information and the use of social information. In high predation, individuals may have a limited time budget to look at what their congeners do and our study indicates that they are more likely to focus on their private information. In addition, the way predators influence the trade-off between the use of private information and the use of social information may vary between species and it would be interesting to see if 9-spine sticklebacks show different use of social information and private information when occurring under varying predation conditions.

Our results also contrast with previous studies (Ward et al. 2011; Ward et al. 2012) in that we found no difference in accuracy between individuals in groups and singletons for fish from populations under high predation. Indeed, fish from those populations showed no significant difference in sampling activity or accuracy between individuals in groups and singletons. Following a wrong

decision, they continued to perform poorly regardless of being alone or in a group. For them, it might be costlier to explore alternative options and after a first negative experience they might be less inclined to engage in further risky exploration. Furthermore, the 2 stimuli looked very similar and the fish may have taken the other stimulus to be nonedible as well and therefore not interesting. An alternative explanation would be that there is variation in competition for food between the high and low-predation sites. Lower portions of rivers—that is high-predation ones—are usually richer in nutrients due to better sun exposition and increased amounts of sediments. This might affect the necessity for individuals in lower locations to consume objects as the streambed may be naturally richer. In such a situation, competition for food may be decreased. However, it is difficult to disentangle from a direct effect of predation.

Fish from high-predation populations were also very consistent following a first correct approach and had a high proportion of subsequent correct approaches (>80% overall), regardless of whether they were alone or in a group. The limited improvement of individuals in groups compared to singletons following a correct decision may be due to the limited potential for improvement. But the high proportion of correct approaches also indicates that they rarely changed toward the nonedible stimulus. One reason could be that after finding a food source, there is little incentive to look elsewhere and change their target after a positive experience of finding an edible object. Additionally for individuals in groups, conspecifics surrounding the other (nonedible) stimulus may have provided social information that the stimulus was not edible, further reducing the incentive to change target. Furthermore, under high predation, exploring for alternative food sources would constitute additional risks. Overall, guppies under high predation seem less likely to change their decision, whether based on their own private information or on social information provided by the other group members. It would be interesting to further investigate this hypothesis as it could be that guppies foraging under high predation are less sensitive to social information, contrary to what has been observed in sticklebacks, *G. aculeatus* (Webster and Laland 2013). The seemingly absence of a cognitive benefit from being part of a group could be due to the cognitive processes being focused on a more urgent problem that the fish were facing, that is predation. Because of this, cognitive power might not be available for solving other relatively less important tasks. Previous work usually focused on increasing the accuracy in one type of task (usually predator detection: Treherne and Foster 1980; Elgar 1989; Ward et al. 2011). In our case, guppies from high-predation populations may use collective cognition advantages and be better at detecting predators but at the cost of responding to and discerning between food sources.

In low-predation populations, accuracy was higher for individuals in groups than for singletons. This performance increase could be attributed to different forms of information use. Individuals that had made a first incorrect decision significantly increased their accuracy in groups as compared to singletons. This could be explained by the significantly higher sampling activity of individuals in groups versus singletons. After a negative experience, individuals in this relatively safe environment were more likely to explore and change toward the other stimulus when part of a group. The higher sampling activity could also be a result of copying/emulation. After seeing other individuals become very active around one stimulus, fish are more likely to come and inspect it several times, as if they may have missed something on the first approach.

In addition, singletons under low predation sampled the nonedible stimulus, despite first finding the edible one and individuals in groups were more accurate than singletons. We found no significant difference in sampling activity between singletons and individuals in groups, suggesting that the difference in accuracy is mostly resulting from the use of social information about the alternative (incorrect) stimulus. The environment in low predation may be safe enough for individuals to explore, which they do when alone but the exploration toward the nonedible stimulus may be reduced by taking into consideration the behavior of conspecifics indicating that the alternative stimulus is not edible and thus not worth investigating. In contrast to high-predation fish, which may have been very good at detecting predators at the expense of discerning food items, guppies from low-predation populations may not pay as much attention to potential predators and benefit from collective advantages that are more foraging-oriented.

Finally, intragroup competition may affect the possibility for an individual to approach a stimulus or switch to another one. On one hand in large groups, the stimulus may be visually obstructed by congeners. On the other hand, high activity around a stimulus may make other individuals curious, even if they are not able to see the stimulus directly.

Previous studies have shown that individuals in groups can outperform single individuals at cognitive tasks, such as detecting and avoiding predators and detecting food patches (Kenward 1978; Cresswell 1994; Lima 1994; Lima 1995; Krause and Ruxton 2002; Ward et al. 2008; Ward et al. 2011). The present study showed that, in contrast to previous work, fish under high-predation risk do not improve their accuracy with group size as compared to fish under lower-predation risk and that the use of private and social information appears to be context-dependent. A more detailed investigation of how private information and social information relatively contribute in collective cognition under varying conditions might be an exciting field for future studies (see Arganda et al. 2012 for a lab study). It would be interesting to further study the mechanisms underlying collective cognition ability of groups to process information in ways that allow their members to benefit from collective cognition when dealing with multiple tasks simultaneously such as detecting a predator and comparing food items. The improvement of groups in foraging accuracy in low predation but not in high predation suggests that collective cognition benefits may be higher for tasks that have a higher impact on individual fitness. Under high predation, the attention is directed mostly toward predator detection and this would be were collective benefits are the most important. Compared to that, finding the better food source is negligible, explaining the poor performance of individuals under high predation. In contrast, in low predation, the attention can be refocused toward foraging, in which detecting the best food source becomes the most important cognitive task.

FUNDING

This study was financially supported by the BehaviourType project granted by the Gottfried-Wilhelm-Leibniz Association's Pact for Innovation and Research (J.K.) and the IGB, from the Champalimaud Foundation (G.dP), and from the Fundação para a Ciência e Tecnologia (Portugal, grant PTDC/NEU-SCC/0948/2014).

The authors thank Josef Antony and Claudia Groen from the Auricher Wissenschaftstage for their support and Philipp Beer, Meint-Hilmar Broers,

