1-2014

Individual Personality Traits Influence Group Exploration in a Feral Guppy Population

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ABSTRACT

We examined whether variation in group exploratory behavior was linked with variation in personality traits (boldness, activity, and sociability) in a population of feral guppies (*Poecilia reticulata*). A huge amount of variation was observed in dispersal tendency between shoals. Surprisingly, no significant correlations were found between group exploratory behavior and average group personality scores, which suggests that the movement of the shoal was not generated by group conformity. However, our analysis revealed correlations between group exploration and the activity score of the least active member of a group and the sociality index of the most social member of a group. These results indicate that a minority of key individuals with certain personality types can have substantial effects on group behavior. These results are discussed in the broader context of group decision making in social animals.

Introduction

A large number of taxa form groups for some or all of their life-history stages. Although there are numerous costs and benefits associate with group living, one of the more fascinating aspects of this behavior is how groups come to make decisions on where to go and what to do (Ioannou et al. 2011). Until relatively recently, much of the research examining group behavior has emphasized the need for group members to adjust their behavior to match the majority. Indeed, a group is typically viewed as a collection of individuals that are all compromising with respect to their own motives to conform to some mean group level behavior (Day et al. 2001; Brown and Laland 2002a). There is great emphasis on conformity within groups because it is well known that predators can single out odd individuals (oddity effect; Landeau and Terborgh 1986). Preferential targeting of odd prey has been documented in a wide range of predators, including mountain lions, hyaenas, and birds of prey (Pienaar 1969; Genovart et al. 2010; Krumm et al. 2010). Predation pressure and the oddity effect create strong selection pressure for conformity within social groups (Couzin and Krause 2003; Galef and Whiskin 2008; Zhou et al. 2009; Ioannou et al. 2012). Thus, there is a strong compulsion for individuals within social groups as fish shoals or bird flocks to remain in close contact and look and behave similarly (conformity effect; Day et al. 2001; Brown and Laland 2002a).

There is emerging evidence, however, that not all members of a group contribute to group behavior equally (Reebs 2000; Couzin et al. 2005; Bode et al. 2012). There may, for example, be leaders and followers within a group and their roles can be defined by a number of motivational and morphological characters. Importantly, there seem to be interindividual differences in the tendency to lead (Leblond and Reebs 2006; Harcourt et al. 2009). For example, dominant individuals may exert a large influence on the behavior of subordinates in a range of taxa including primates (Leca et al. 2003). Individuals are also more likely to associate with, and therefore follow, familiar individuals as opposed to strangers (Swaney et al. 2001). In shoals of fish, we have long known that a minority of knowledgeable demonstrators within a group can encourage the rest of the group to maintain seemingly random behavioral patterns (Reebs 2000; Swaney et al. 2001; Ward et al. 2008). Moreover, these behaviors can be maintained by the group even after the demonstrators are removed from the group or when the behavior becomes maladaptive (Laland and Williams 1997, 1998). The mechanism whereby this occurs seems to be relatively simple. Noninformed or unmotivated individuals prioritize schooling, whereas motivated or informed individuals balance the need for schooling and the desire to move in a particular direction (Couzin et al. 2005). In this way, the group remains a cohesive unit and tends to move in the direction desired by just a few individuals. As group size increases, the proportion of motivated individuals required to control group behavior tends to decrease. Research examining the emergent properties of group behavior in humans has also shown that just a few key individuals that are motivated to move in a particular direction can exert a disproportional influence on the movement of the group as a whole (Dyer et al. 2008, 2009b).

Personality traits have become an increasingly popular mechanism for understanding consistent individual differences in behavior and have broad evolutionary and ecological consequences (Sih et al. 2012; Wolf and Weissing 2012). It is likely that individuals that differ in their personality traits might also exert varying influence on group behavior. Although individual personality trait can determine how individuals move in space (Fraser et al. 2001), a handful of studies have examined the relationship between the movement of the group and average group level traits (Blumstein et al. 2009; Cote et al. 2011; Fogarty et al. 2011). These studies have shown that individual dispersal tendencies do not just depend on the personality of the individual but also on variation in afilliative behavior, the mixture of behavioral types within a population, or even an interaction between group personality and the personality of the disperser. For example, Cote et al. (2011) found that the dispersal tendency of individual fish (*Gambusia affinis*) was determined by the average boldness and sociability score of their population. Regardless of their own behavioral type, individuals from populations with more asocial or bold individuals dispersed further.

Many fish species form shoals for some part of their lives. Guppies are a social species, foraging in small, loosely organized shoals and show facultative schooling behavior in response to predation pressure (Lachlan et al. 1998). Fish shoals have often formed the focus of studies elucidating the decision rules used by individuals with a group with a view to understanding how these ultimately influence group behavior (Ioannou et al. 2011). The use of fish shoals to study group behavior undoubtedly stems from their incredible schooling displays where thousands of individuals seem to move as a single fluid whole. Fish have also been a key model for examining animal personality traits (Budeav and Brown 2011). Personality traits such as boldness, activity, and aggressiveness are often correlated with one another in various syndromes (Dingemanse et al. 2007; Irving and Brown 2013). Previous studies have demonstrated a link between certain behavioral types and measures of fitness in guppies, including mate choice (Godin and Dugatkin 1996), predator deterrence (Godin and Davis 1995), and survival (Smith and Blumstein 2010). There are good reasons to suspect that individual variation in behavior influences the behavior of the group as a whole. For example, groups comprised of shy and bold fish were faster to explore a novel arena and sample a foraging patch than those containing only shy or only bold individuals

(Dyer et al. 2009a). In contrast, one might predict that highly inactive fish could anchor the social group to a single location in a form of negative inhibition (Brown and Laland 2002b).

Using a population of feral guppies (*Poecilia reticulata*), we examined the extent to which key individuals exhibiting certain personality traits contributed to group exploratory behavior in a novel arena. We had the expectation that group behavior would be better explained by the personality of these individuals rather than by the average personality traits of all individuals in the shoal (i.e., group conformity). That is, these key individuals would unduly influence shoal behavior.

Methods

Subjects and behavioral measures

Feral guppies (*P. reticulata*) were collected from Fannie Bay, Darwin, in May 2011, using dip nets, packed in sealed bags, and airfreighted to the Central Animal House at Macquarie University in Sydney, New South Wales. The collection site was a freshwater drainage ditch adjacent to Fannie Bay racecourse, which leads downstream to an estuarine creek containing large piscine predators. This population is thus periodically exposed to large numbers of predators, which arguably produces the highest level of antipredator behavior in fishes (Ferrari et al. 2008).

We used a total of 80 (40 males and 40 females) guppies in this study, with all tests carried out between August 2011 and February 2012. To facilitate individual recognition, males and females were housed in single sex shoals of 10 individuals in a series of aquaria (38 × 21 cm and 28 cm deep). Each aquarium was furbished with river gravel and Java moss to provide shelter, with water quality maintained using an internal power filter and monthly water changes. Fish were fed commercial flake food (Tetramin tropical flakes) once daily and offered bloodworms and lettuce on occasion for variety. The room was heated to 25°C and maintained on a 12-h photoperiod (lights on at 0700 hours). To permit individual identification, females were lightly anesthetized using 0.1 g/L MS-222 (tricaine methanesulfonate; Sigma-Aldrich) with a sodium bicarbonate buffer and injected with elastomer tags (Northwest Marine Technology). Fish recovered from anesthetic within 2 min. We used 3 colors (orange, yellow, and green) injected into 1 of 4 locations (front left, front right, back left, and back right) to provide 12 unique tag combinations that were repeated in each group. Tagging and anesthetic had no effect on behavior, and all fish recovered fully. Males were photographed on their left side and sketched using an outline template to chart their unique pattern of coloration. In particular, the orange carotenoid and black melanin spots, in addition to the shape of the caudal and dorsal fins, provided stable individual characteristics. The handling stress induced by procedures performed on each of the sexes was likely to be similar, and fish had ample time to recover prior to testing. For all individuals, standard length (SL; the distance from the tip of the snout to the caudal peduncle) was measured to the nearest 0.1 mm using calipers.

Following tagging and measurement, the fish were given a week to recover, and we then exposed them to several personality assays as outlined in Irving and Brown (2013). The time between each context was approximately 7 days.

Personality assay 1: boldness

The experimental arena consisted of a large aquarium (91 × 51 cm and 20 cm deep) with 12 cm of water and 2 cm of gravel. Plastic plants, marbles, stones, and Duplo® (http://duplo.lego.com) were scattered throughout the arena to create a novel testing environment. A starting box constructed of black Perspex (9.5 × 7.5 × 14.5 cm) was positioned on a white plastic semicircle (9 cm radius) at the far end of the aquarium (Figure 2). The box was fitted with an opaque lid and a sliding trapdoor, which could be opened remotely via a piece of fishing line (sensu Brown et al. 2007b). A heater was placed at the far end of the

arena and set to maintain a water temperature of 25 °C. Observations were taken from behind the starting box so as not to influence emergence times.

Each fish was contained in the starting box for an initial settling period of 2 min. The trapdoor was then gently lifted, with boldness measured as the time taken to cross the white semicircle onto the gravel arena (Brown and Braithwaite 2004; Brown et al. 2007a; b). If the subject had not emerged after 6 min, the opaque lid was removed from the starting box to encourage exploration. At 8 min, the trial was terminated, and the subject awarded a maximum possible score of 480 s. Only 2 fish did not emerge from shelter. We tested a total of 40 male and 40 female guppies for boldness twice, with a minimum period of 7 days between each trial. The experimental arena was refurbished between trials in order to maintain a novel testing environment.

Personality assay 2: activity

Activity levels were measured in 10 replicate aquariums (44 × 24 cm and 24 cm deep) filled with 2 cm of gravel and 19 cm of water. A 6.2 × 6.2 cm grid (7 squares wide and 3 squares high) was drawn on the front surface of each aquarium. The tanks were visually isolated from one another via blue backing on their adjoining walls. The room temperature was set to 25 °C to ensure water temperature was constant throughout the testing period. To prevent any observer-induced bias, observations were taken from behind a curtain using a webcam placed in front of the grid.

A single fish was randomly assigned to each aquarium and introduced the day before testing to allow them to habituate to their surroundings. Activity was recorded each time a fish crossed a grid line over a 10-min period using the behavioral transcription program EthoLog v2.2.5 (Ottoni 2000). All tests were carried out between 1100 and 1300 hours, and the order in which the fish were tested was randomized. We tested a total of 40 female and 40 male guppies twice for activity, with a minimum period of 48 h between each trial.

Personality assay 3: sociability

We recorded sociability, a relatively poorly studied trait, in place of aggression because we could not reliably illicit aggressive responses from females. An inverse relationship between aggression and schooling tendency has been demonstrated in a previous study on guppies (Magurran and Seghers 1991).

The apparatus consisted of a small aquarium (22 × 15 cm and 15 cm deep) placed inside one of the aquariums used for testing activity (44 × 24 cm and 24 cm deep) to create a transparent physical partition. A shoal of 6 unfamiliar female guppies was selected from a large pool of fish and placed into the smaller tank, allowing visual but not physical or chemical contact with the larger tank. Although it is possible that some individuals were repeatedly used in the target school, it is extremely unlikely given the size of the pool (n = 50). The water level was maintained at 12 cm to prevent escape of the shoal. The room temperature was set to 25 °C to ensure water temperature was constant throughout the testing period. Observations were taken from behind a curtain using a webcam placed in front of the grid. Sociality was measured as the proportion of time spent in proximity to the shoal over a period of 10 min using the EthoLog v2.2.5. We divided the length of the tank into 5 regions (6.2 cm wide), where "A" was the column closest to the shoal and "E" was the furthest column away. Each fish was placed into the far end ("E") of the larger aquarium and given 5 s to settle before timing began, with the order of testing randomized. We tested a total of 40 female and 40 male guppies twice for sociality, with a minimum period of 48 h between each trial.

Group exploratory behavior

The exploration experiment was conducted in 2 identical apparati, each consisting of 3 plastic storage containers (31 × 48 cm and 31 cm deep) connected end to end via 2 lengths of PVC pipe (8 cm × 35 mm) secured with black aquarium silicone (Figure 1). A submersible pump (400 L/h) was placed in the first container and run to the outermost via a 2 m length of 13-mm polyvinyl tubing so as to create a current through the system. Thus, each of the 3 pools was separated by a "riffle," and fish had no problem traversing the riffles in either direction. Water depth was maintained at 22 cm, and each container was furbished with 2 cm of river gravel and plastic plants to provide shelter. The room temperature was set to 25 °C to ensure water temperature was constant throughout the testing period.

On the morning of each test, 2 shoals consisting of 4 individuals (2 males and 2 females) were randomly selected from their housing tanks, individually identified, and placed into the central container of each apparatus. The position of each fish (upstream, central, or downstream container) was recorded at 20-min intervals for 6 h, after which the subjects were returned to their home tanks. Observations were taken directly through the transparent containers. These observation periods were kept brief to avoid disturbing the fish. We tested exploratory tendency in a total of 20 shoals comprising 40 male and 40 female guppies. All tests carried were out between 0900 and 1500 hours in February 2012. As with the behavioral measures outlined above, room temperature was maintained at 25 °C and monitored daily with a thermometer to ensure consistent testing conditions. The apparatus was lit evenly from 2 m above with fluorescent lighting.
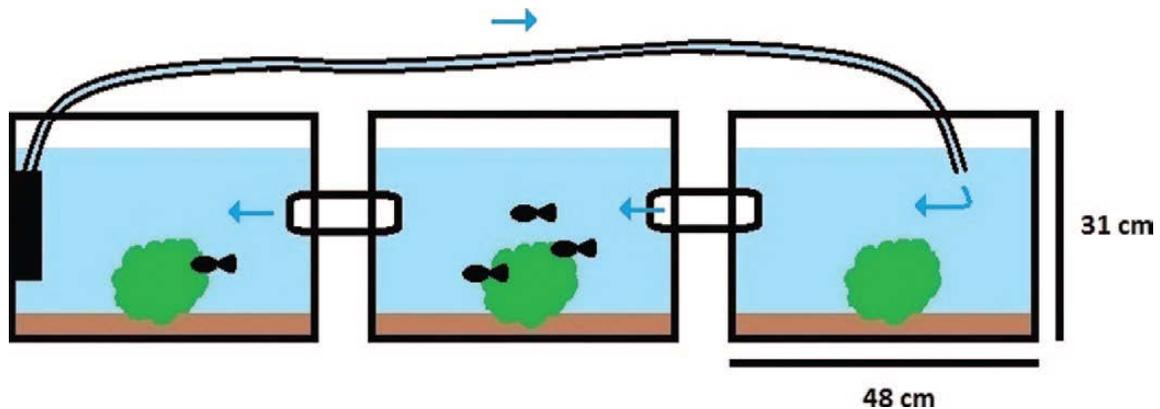

Figure 1. Diagrammatic representation of the apparatus. Subjects were placed in the central container and their movements recorded with respect to their position in the current (downstream, central, or upstream). Blue arrow illustrates the direction of the current.

Statistical analysis

The boldness, activity, and sociability data required a natural $\log(y + 1)$ transformation to satisfy the assumption of normality. Because boldness was measured as the time taken to emerge from shelter into a novel environment, higher boldness scores indicate shyer individuals. We generated a "sociability index" (SI), where SI = $1000/\Sigma$ [(time spent in column x) × (distance of column x from the shoal + 1)]. SI is a continuous variable with higher scores indicating more social individuals. Spearman rank correlations were used to assess the consistency of the behaviors between trials. We conducted repeatability tests on

each of the 3 traits for males and females separately. We used the average scores of each individual for boldness, activity, and sociability in our correlations with group exploratory tendency.

Exploratory tendency was calculated as the total number of movements between containers at the individual level. The average number of movements between containers for each group was then used to calculate group exploratory tendency. In the first instance, individual exploratory tendency was examined using a general linear mixed model (GLMM) where sex was set as a fixed factor and group identity as the random factor. The main point of this analysis was to compare group and individual level variability. Between group variation in exploratory tendency was very high (see Results), so we analyzed the relationship between group exploratory tendency, mean personality scores, and the 2 extreme personality scores in each group using multiple regression in StatView v5.0.1. Three analyses were conducted, one for each of the 3 personality traits.

Having identified that key individuals within the group control exploration tendency, when then examined how these individuals contributed to social dynamics as the fish moved around in the flume. To do this, we tabulated how often singletons were observed, how often all 4 fish were found in the same compartment, and the mean elective group size of each shoal over the observation period.

Results

The influence of SL had to be examined within sexes because males are smaller than females, and thus these 2 variables are confounded. Within the sexes, SL was not significantly correlated with any of the variables measured ($P > 0.05$). Both sexes demonstrated rank consistency between trial 1 and trial 2 for all of the personality variables, which is indicative of personality traits (Table 1). Repeatability indices were generally higher for females than for males (Table 1). There was evidence of behavioral syndromes involving all 3 traits in males but not in females (for details, see Irving and Brown 2013).

Results of the GLMM revealed no evidence of a difference in exploratory tendency between the sexes ($F_{1,19} = 0.002$, $P = 0.965$) or an interaction between groups and sex ($F_{19,40} = 0.867$, $P = 0.622$). The vast majority of the variation was defined by group identification ($F_{19,40} = 14.56$, $P < 0.001$), which was independent from testing order (Figure 2). Thus, the random sampling did not generate variation in the average level of personality traits in the shoals.

Multiple regression showed that exploration in the flume was related to activity scores ($F_{3,16} = 4.783$, $P = 0.014$; Table 2). Within the activity scores, only the least active individual influenced exploratory tendency ($t = 3.050$, $P = 0.007$; Figure 3). Groups that explored the least were those in which the least active members had comparatively low activity scores. While overall, the sociability scores did not influence exploratory behavior ($F_{3,16} = 2.148$, $P = 0.134$). Within the sociability scores, the most social individual influenced exploratory tendency ($t = 2.416$, $P = 0.028$; Figure 4). Groups that explored the most were those in which the most social members had a comparatively high sociality index. None of the boldness scores influenced exploration tendency in the flume ($F_{3,16} = 0981$, $P = 0.426$; Table 2).

When analyzing how these key individuals in the group influence the social behavior of the shoal while in the flume, we found that the least active members were associated with high elective group sizes ($F_{1,19} = 6.000$, $P = 0.025$) and a high propensity for all members of the school to be found in the same location ($F_{1,19} = 6.396$, $P = 0.021$). In contrast, highly social individuals were associated with a low propensity for all individuals to be found in the same location ($F_{1,19} = 4.428$, $P = 0.049$).

Fish spent a large proportion of their time together as a single group (46% of the time), and singletons were rare (just 11% of observations). The mean elective group size over the entire study was 3. There

was no differences between the sexes for any of these metrics. Thus, this population of guppies is highly social, which is perhaps not surprising given their high predation origin.

Table 1. Spearman rank correlations (r_s), associated *P* values, and repeatability scores for repeated tests of the 3 behavioral measures in male and female guppies

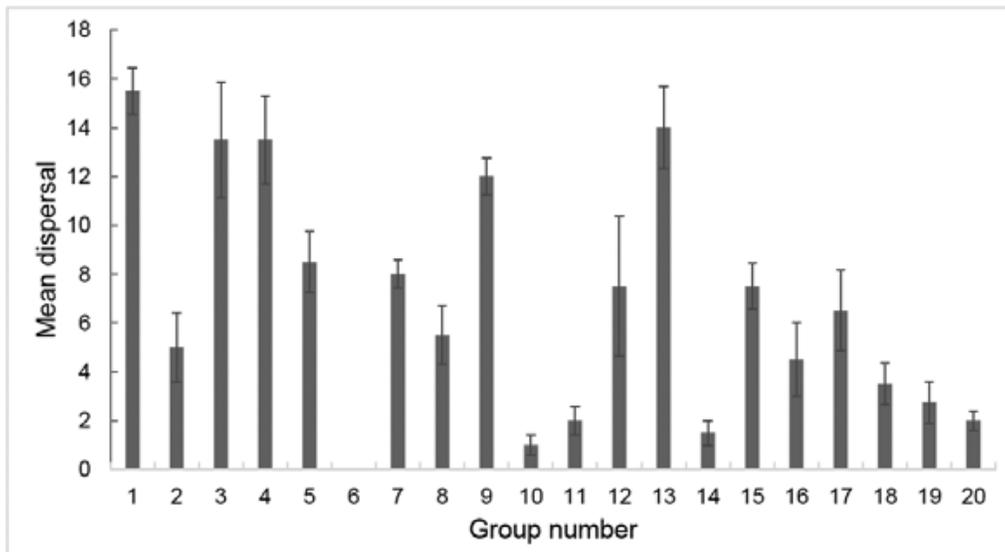|	Females			Males		
Trait	*r_s*	*P*	*R*	*r_s*	*P*	*R*
Boldness	0.509	0.002	0.43	0.361	0.024	0.22
Activity	0.453	0.005	0.38	0.396	0.013	0.28
Sociability	0.406	0.011	0.46	0.563	0.000	0.47

Figure 2. Exploration tendency (average number of movements per group ± standard error) across the 20 guppy shoals, each comprising 4 individuals (2 males and 2 females) of known personality.

Table 2. *P* values for the multiple regression models examining the mean group exploratory behavior

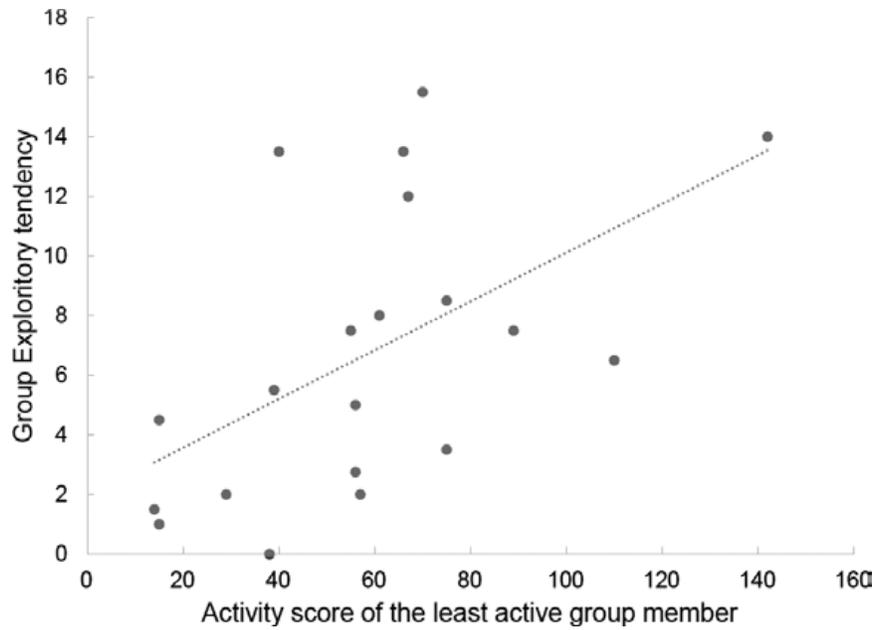| Traits	Full model *P*	Average trait *P*	Highest trait *P*	Lowest trait *P*
Boldness	0.426	0.506	0.524	0.236
Activity	0.014	0.226	0.757	0.007
Sociability	0.134	0.845	0.218	0.028
The full model, group average personality score, individual with the highest personality score in the group, and the individual with the lowest personality score in the group.				

Figure 3. The positive correlation between group exploration and the activity score for the least active member of that group. Multiple regression: $t = 3.050$, $P = 0.007$.
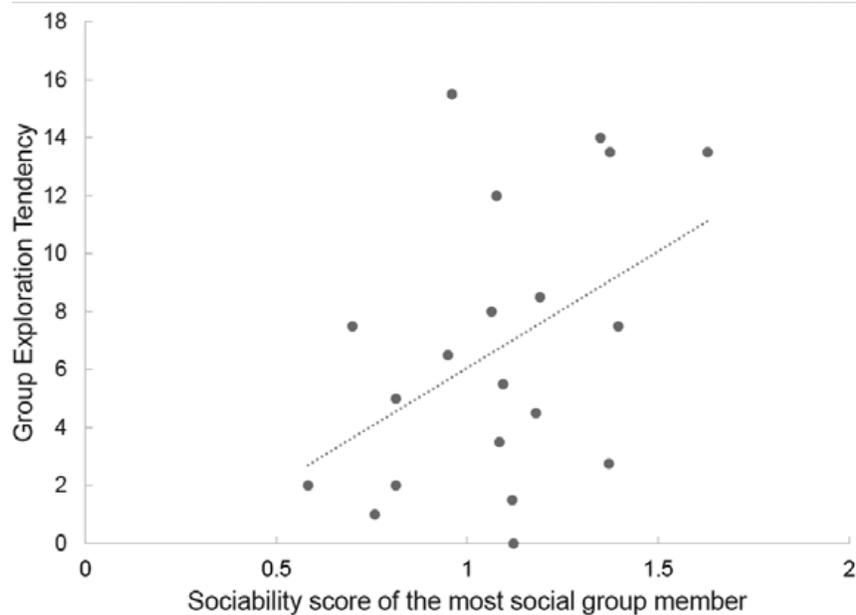

Figure 4. The positive correlation between group exploration and the sociality score of the most social member of that group. Multiple regression: $t = 2.416$, $P = 0.028$.

Discussion

Examination of the exploratory behavior of guppies in small shoals was dominated by between-group variation. Surprisingly, no significant correlations were found between group exploratory behavior and any of the group mean personality scores (boldness, activity, and sociability). Rather, the exploratory behavior

of the shoal was controlled by the personality traits of key individuals within the shoal (sensu Couzin et al. 2005). Correlations were found between group exploratory behavior and the activity score of the least active member of a group (Figure 3) and the sociability score of the most social member of a group (Figure 4). The results of this study show that key individuals within the shoals had substantial effects on the behavior of the group as a whole, with group exploration retarded by their least active group member and encouraged by their most social group member.

A major dilemma faced by individuals in social groups is deciding what to do and when to do it. An important issue, however, is how individuals within a group reach consensus about the type and timing of certain activities in order to generate this conformity (Van Vugt 2006). In agreement with our findings, many studies report that key individuals can strongly influence group decisions, with the rest of the group simply following their lead (Dyer et al. 2009b; Kurvers et al. 2009; Bode et al. 2012). Because information is distributed unevenly within groups of social animals, these leaders are often highly motivated, informed individuals with knowledge of a particular migration route or the location of a reliable food source (Lachlan et al. 1998; Reebs 2000; Reader et al. 2003). Dyer et al. (2008) demonstrated that in human crowds, a small number of informed individuals can increase the speed and accuracy of group movement without the need for verbal communication or active signaling. Furthermore, Couzin et al. (2005) used computer simulations to show that consensus decisions can be reached even when informed individuals do not know whether they are in the majority or minority.

Although leadership has frequently been attributed with experience and dominance (Reebs 2000; Šárová et al. 2010; Bode et al. 2012), evidence is emerging that leaders may also differ in terms of their personality (Johnstone and Manica 2011). For example, there is a correlation between personality traits and rank in a dominance hierarchy in rainbowfish (Colleter and Brown 2011), and dominant individuals often act as effective demonstrators thereby having undue influence over the behavior of the group (Coussi-Korbel and Fragaszy 1995). In the context of group movement, individuals at the forefront of the group may be at an advantage in terms of foraging, but they are also more vulnerable to predation owing to their position. These differences in the relative costs and benefits of leading and following have prompted the suggestion that leaders may have intrinsic differences in personality compared to followers (Kurvers et al. 2009).

Kurvers et al. (2009) revealed a significant relationship between leadership and boldness in barnacle geese (*Branta leucopsis*). Irrespective of dominance rank or body size, barnacle geese that were bolder toward a novel object were more likely arrive first at a food patch. No relationship was found between leadership and activity or exploration in an open field test, suggesting that not all aspects of the leader's personality influence group behavior. Moreover, Bode et al. (2012) reported that individuals with strong social connections were more likely to be followed by other group members. Similarly, we found that guppy shoals that explored the apparatus most thoroughly were those in which the most social members had a comparatively high SI. Key individuals can also have substantial negative impacts on the group. The presence of hyperaggressive males in groups of water striders, for instance, reduced group reproductive success (*Aquarius remigis*) (Sih and Watters 2005). This is similar to our finding that the shoals that moved the least were those in which the least active members had comparatively low scores for total activity, with the failure of 1 individual to move triggering negative feedback within the group. Negative social reinforcement has also been shown in foraging contexts in fishes (Brown and Laland 2002b).

Importantly, no correlations were found between group exploratory behavior and any of the group average personality scores (boldness, activity, or sociability) in our feral population of *P. reticulata*, providing confidence that the massive variation in dispersal tendency between shoals we observed was driven by a minority of key individuals not by group conformity. This contrasts with the findings of Cote et

al. (2011), which revealed a significant relationship between dispersal tendency and group personality in mosquitofish (*G. affinis*). Individual mosquitofish from populations with higher boldness scores or lower sociability scores were more likely to disperse irrespective of their own personality. Although, in this study, we monitored movement continuously in the laboratory using shoals of 4 individuals, Cote et al. (2011) measured dispersal distance in an artificial stream using shoals of 30 or more individuals. Although it is possible that the shoal sizes chosen by Cote et al. (2011) were too large for key individuals to exert influence over the majority, Couzin et al. (2005) demonstrated that the proportion of informed individuals required for accurate navigation actually decreases with increasing group size. The small shoal size used in this study, however, is consistent with that of wild guppies, giving ecological relevance to our results (Smith and Blumstein 2010). It may be that the variation in the schooling behavior of these 2 invasive species gives rise to different social dynamics. Nevertheless, future studies investigating personality-dependent movements in *P. reticulata* should examine a range of group sizes in order to determine whether the influence of key individuals is magnified, reduced, or unchanged.

Funding

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