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ARTICLE

The relationship between personality and the collective motion of schooling fish

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Abstract

The personalities of schooling fish members are thought to have profound effects on group behavior, indicating that group members must maintain their personality to some extent. However, whether and to what extent personality traits are maintained or sacrificed during schooling has seldom been investigated. Thus, we aimed to verify the possible correlation between an individual's personality traits and its movement characteristics during schooling. We first measured the boldness, exploration, activity and sociability personality traits of pale chubs (*Zacco platypus*). Then, we randomly divided the individuals into ten groups containing six members and measured their movement characteristics. In factor analysis, boldness and activity variables could be reduced to a single factor, and two variables related to sociability and one variable related to boldness (time spent outside the shelter) could be reduced to a single factor. The correlation between factor scores and collective motion traits showed that proactive pale chubs (with greater boldness and activity) swam with higher polarity with the centroid of the group than did reactive individuals, and individuals with higher sociability were more synchronized with the group centroid in terms of swimming speed. These findings suggest that proactive individuals have a greater alignment tendency and might have an advantage of efficient information transfer, enabling them to gain more synergistic benefits as group members than reactive individuals. The present study, along with information from our recent study, suggests that variation in the personality (especially boldness and sociability) composition of fish groups might be a major cause of variation in group-level behavior.

Keywords Boldness · Sociability · Personality · Schooling

Animal personalities are defined as consistent individual differences in behaviors across time and contexts (Réale et al. 2010; Wolf and Weissing 2012; Killen et al. 2016; Tang and Fu 2019; Lloren et al. 2019). Animals are thought to exhibit different behavioral syndromes, as proactive individuals are usually bolder and more explorative but less sociable than reactive individuals (Martins and Bhat 2014). The maintenance of personality types is thought to be of vital ecological relevance in fish species (Sih et al. 2012; Jolles et al. 2017; Knebel et al. 2019), as individuals with different personalities exert varying influences on group behaviors such as decision making (Harcourt et al. 2009) as well as the cohesion and alignment of collective motions (Cote et al. 2011; Jolles et al. 2018; Planas-Sitja et al. 2018; Tang and Fu 2019). If so, the behaviors of group members should vary, and individuals might withhold some of their behavioral traits when joining a group. However, a study also found that individuals can only partly maintain their spontaneous swimming traits when measured alone, whereas such individuality decreased profoundly with an increase in group size (Herbert-Read et al. 2013). This finding suggests that group members might compromise their personality when conflict arises between their group mates to function effectively and cohesively. Thus, how fish group members adjust their personality in response to group moving direction alignment and synchronization of swimming speed might be of utmost importance in the field of animal behavior (Jolles et al. 2017; Knebel et al. 2019).

Previous studies aiming to test for personality maintenance in a group usually involved variables indicative of activity, such as median swimming speed and the body-turning rate, as such variables can be measured under both

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collective and solitary conditions (Herbert-Read et al. 2013). However, as scientists have found that boldness and exploration tendency have important effects on collective motion (Brown and Irving 2014; Tang and Fu 2019), a detailed investigation on the possible linkage between personalities measured individually and the behavior of individuals within a group might provide interesting results. Furthermore, studies have revealed that the mechanisms underlying personality traits might differ according to their effect on collective motion. For example, the effect of the activity score of group members on collective motion might depend on the majority, as such motion reflects the average activity levels of the group members. However, the effect of the boldness score of group members on collective motion might be decided more by a minority of the group members, since collective motion is most affected by the individuals exhibiting the least boldness (Tang and Fu 2019). Thus, we assumed that behavioral studies of groups of fish individuals and comparisons between singletons and groups might yield interesting outcomes. Therefore, the present study aimed to investigate the relationship between traditionally measured personality traits measured in singletons and the collective motion traits of each group member.

To this end, we used movement traits of all group members and traditional measurements of personality in a fish species. We measured the personality levels of 60 individuals and then measured movement characteristics of each individual in groups, such as the median swimming speed, body-turning rate, synchronization of swimming speed with the speed of the group centroid (SS), separate swimming angle in comparison to that of the group centroid (SSA), and distance to the group centroid (DGC). We then performed a factor analysis to reduce the personality data to a small number of explanatory factors (three individual personality scores in the present study), as frequently performed in personality studies (Colchen et al. 2017, 2020; Sumpter et al. 2018) and correlated them with collective motion traits. We used the pale chub (*Zacco platypus*) in the present study because this species prefers to live in groups and previous studies have shown that it possesses high morphological and physiological variation (Johansson 2006; Fu et al. 2013, 2015).

Materials and methods

Experimental animals

Sixty juvenile pale chubs [body mass 6.37 ± 0.15 g; mean ± standard error (SE)] were seine fished by local fishers from a tributary of the Wujiang River (29°24′37″N, 107°31′55″E, Wulong County, Chongqing city). All fish were maintained together in a 250 L rearing system with aerated water. Twenty percent of the water was exchanged with freshwater daily. The water temperature was maintained at 25 ± 0.5 °C. The photoperiod was 12 h light 12 h dark. The pale chubs were hand fed to satiation once daily (at 8:00 am) for four weeks with tubifex worms. The feces and uneaten tubifex worms were removed with a siphon at 9:00 am. The dissolved oxygen level of the water was maintained above 7 mg L^{-1}. After 4 weeks of acclimatization, experimental fish were tagged intraperitoneally with passive integrated transponder (PIT) tags under anesthesia by neutralized tricaine methane sulfonate (50 mg L^{-1}). All experimental individuals were used to measure personality traits and collective motion.

The present study was authorized by the Animal Care and Use Committee of the Key Laboratory of Animal Biology of Chongqing (permit number Zhao-20161124-03).

Experimental protocol

One week after being tagged with PITs, the individuals were labeled by visible implant fluorescence (VIF) and allowed to recover for 1 week; then their personality variables, including boldness, exploration, activity and sociability (see details below), were recorded. The recordings were conducted in four identical arenas (see details in "Experimental setup") at the same time, from 8:00 am to 17:00 pm. The arenas were cleaned after the measurement of each fish. After measuring the personality variables, we randomly divided the individuals into ten groups of six and measured their movement characteristics. Body mass and body length were measured after collective motion measurement.

Experimental setup

We used a rectangular tank (length × width × height: 70 × 35 × 35 cm) as the arena to measure personality traits of boldness, exploration and activity, as in previous studies (Liu and Fu 2017; Fig. 1a). The arena was surrounded with a white opaque canvas to minimize external stimulation, and the walls of the arena were covered with white paper. The arena was separated into two subareas by a white opaque partition that was used to separate the open area (length × width × height: 55 × 35 × 35 cm) from a shelter area (length × width × height: 15 × 35 × 35 cm), which provided a refuge with artificial plants. A small door (width × height: 10 × 10 cm) on the partition allowed fish to move freely from the shelter area to the open area when the boldness was measured, but it was closed when the exploration and activity were measured. The water depth was 10 cm during measurement. The behaviors of the fish were video recorded by a webcam (Logitech Pro 9000; Logitech Company, Suzhou, China) located directly above the tank.

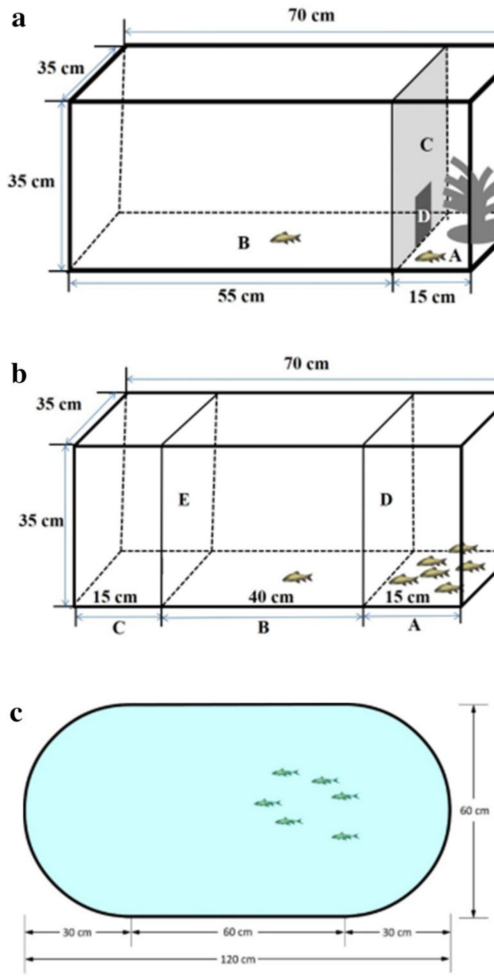


Fig. 1 Design of the experimental arena used for personality measurement (**a**); **a** shelter area (length × width × height: 15 × 35 × 35 cm); **b** open area (length × width × height: 55 × 35 × 35 cm); **c** opaque partition; and **d** small door. Design of the arena used for the measurement of sociability (**b**); **a**, **c** stimulus area; **b** test area; **d**, **e** transparent partition. Design of the experimental arena used for the measurement of collective motion (**c**)

Sociability was also measured in a rectangular tank arena (70 × 35 × 35 cm), which was the same as that used in previous studies (Killen et al. 2016, Fig. 1b). Transparent partitions separated the tank into two stimulus areas (15 × 35 × 35 cm) on the right- and left-hand sides and a test area in the middle (40 × 35 × 35 cm). We covered the walls of the arena with white paper, except for the partition between the test and the stimulus areas, and surrounded the tank with a white opaque curtain to minimize the effect of the observer. The water depth was 10 cm during measurement. The movements of the test fish were video recorded by a webcam located directly above the tank.

Measurement of personality

Boldness A fish was transferred into the shelter area and preacclimated for 30 min; then, the small door was gently opened by a remotely operated line, and the behavior of the fish in the open area was video recorded for 30 min. The total number of experimental fish entering the open area (i.e., number of inspections, NOI) during the period and percent time in the open area (PTO) were used to measure boldness. If the fish showed a large NOI and high PTO, it was regarded as a bold individual. Importantly, the variables associated with boldness are closely related to those associated with exploration, and the NOI and PTO might also be indicators of exploration (Sih et al. 2012). In addition, the fish behavior may have been affected by phototaxis due to the difference in light intensity between the shelter and open areas, but the effect was the same for all individuals. Of the 60 individuals, we excluded three individuals from the analysis because of broken video files.

Exploration After recording boldness, the fish that stayed in the shelter area were gently guided by a hand net to the open area of the arena and acclimated for 10 min with the small door between open and shelter areas closed. Then, a novel object (a sinking black plastic ball with a diameter of 2 cm) was carefully placed in the tank with a hand net at a distance of 40 cm away from the small door (Fig. 1), and the movements of the fish were recorded by the webcam for 10 min. The time at which the novel object was first encountered (the first time the fish moved within 7 cm of the object, FTO) and the minimum distance to the novel object (MDO) were used to measure exploration. If the fish showed an early FTO and short MDO, it was regarded as an exploratory individual.

Activity After recording exploration, the novel object was carefully removed by a hand net, and the fish was again acclimated for 10 min to eliminate the effect of the exploration context. Then, the spontaneous movements of the fish were recorded by the webcam for 10 min. The percent time spent moving (PTM) and median spontaneous swimming speed were considered indicators of activity. If the fish showed a high PTM and fast swimming speed, it was regarded as an active individual. The test tank was cleaned, and the water was changed after each measurement.

Sociability Sociability was evaluated as the preference of the experimental fish for staying with stimulus shoals (six individuals in the stimulus area vs. the empty area) immediately after the measurement of activity. Stimulus individuals composed of naïve fish were first transferred to the stimulus area (alternating between the left and right areas), and then after 5 min, the fish tested for sociability was transferred to the test area. Then, the behavior of the test individual was video recorded for 15 min. Sociability was calculated as the percentage of time that the test individual stayed within

20 cm (a distance three times the body length of the fish, Miller and Gerlai 2008) of the stimulus area (PTS) and the average distance to the stimulus shoal (i.e., the middle of the partition, DTS) (Killen et al. 2016). If the fish showed a low PTS and short DTS, it was regarded as a sociable individual. The test tank was cleaned, and the water was changed after each measurement. All individuals were transferred to a 250 L rearing system, which was the same as that used during the preacclimation for latter collective motion measurement.

Before data processing, we first converted the videos from.wmv to.avi format (Format Factory, https://format-factory.softonic.cn). Then, the videos were imported into EthoVision XT9 (Nodus, Netherlands). This program automatically calculated the x and y coordinates of the test individual. Then, we calculated the PTM as a swimming speed higher than 1.75 cm s^{-1}. We eliminated movements with speeds less than 1.75 cm s^{-1} to minimize potential system noise and small movements of the animal (body wobbles) according to previous studies (Tang et al. 2017; Tang and Fu 2019). The speed (v, cm s^{-1}) was calculated as follows:

$$v(t) = \sqrt{(x(t) - x(t-1))^2 + (y(t) - y(t-1))^2}/d, \quad (1)$$

where $x(t)$ and $x(t-1)$ and $y(t)$ and $y(t-1)$ are the coordinates of the tested fish at time t and the time of the previous frame $(t-1)$ and d is the length of the time interval. FTO was defined as the time when the test fish first moved within 7 cm (one body length) of the novel object. Other variables were calculated according to the coordinates of the experimental fish and the novel object (for the measurement of MDO) or partition (for the measurement of DTS) or quantified on the basis of the sequence of the coordinates of experimental fish (for the measurement of variables other than those mentioned above) as in previous studies (Tang and Fu 2019). Fish were not fed on the day that the personality variables were measured, and all personality variables were measured two times over 2 days. The mean of these two values was used for further analysis.

Measurement of collective motion

Grouping and recording We used a white, rounded, rectangular tank (length × width × height: 120 × 60 × 35 cm, Fig. 1c) as the arena to measure the collective motion of fish groups. The water depth was 10 cm during measurement. Sixty fish were randomly divided into 10 groups of six individuals. We used the collective motion of six individual groups, as previous studies found that a group composed of more than four members showed typical group-level characteristics (Tang et al. 2017). A webcam mounted directly above the arena recorded videos of the motions of the groups. The group members were introduced to the experimental arena at 8:00 am without having been fed and acclimated for 30 min. Then, 30 min videos of the collective motion of each group were recorded four times every 2 h from 8:30 to 15:00, i.e., 8:30–9:00, 10:30–11:00, 12:30–13:00 and 14:30–15:00 (fish remained in the experimental arena during the interval between videos). The locomotive trajectories were then analyzed, and the mean value was used for further analysis.

Collective motion The videos were imported into idTracker (v 2.1) after format conversion, which automatically discriminated all group members and calculated the x and y coordinates of each group member (see details in Pérez-Escudero et al. 2014). Then, group members were further identified by the combination of VIF and PIT. Of the 60 individuals in the ten groups, two were excluded from the analysis due to technical problems. The trajectories of the remaining 58 individuals were smoothed by a weighted moving average with a 0.5 s window (Miller and Gerlai 2012). The activity of each group member was assessed according to the median speed (V_{group}) to address the personality traits associated with activity. Swimming coordination was measured according to the synchronization of speed (SS) between each group member and the group centroid as follows (Delcourt and Poncin 2012):

$$SS_v = 1 - \left| \frac{v_i - v_j}{v_i + v_j} \right|, \quad (2)$$

where v_i and v_j are the speeds of the experimental fish and the group centroid (i.e., the mean of the x and y coordinates for all six group members), respectively.

The DGC (distance to the group centroid, cm) was used to evaluate cohesion and was calculated as follows:

where

$$D_{ij} = \sqrt{(x_i - x_S)^2 + (y_i - y_S)^2} \quad (3)$$

and x_i and y_i and x_s and y_s are the coordinates of any group member and the group centroid, respectively.

The separate swimming angle (SSA) was defined as the difference in the angle between the vector of each group member and the vector of the group centroid. Vector (A) was calculated as follows:

$$A = \arctan \frac{y(t) - y(t-1)}{x(t) - x(t-1)}, \quad (4)$$

where $x(t)$ and $y(t)$ are the coordinates of any group member or the group centroid, and $x(t-1)$ and $y(t-1)$ are those in the previous frame, respectively.

The body-turning rate was defined as the absolute change in the body center (see details in Herbert-Read et al. 2013 and Sumpter et al. 2018).

Data analysis

One-sample Kolmogorov–Smirnov test results indicated that all the variables were normally distributed. We used SPSS 17 for data analysis. Data are presented as the means ± SEs, and P values no higher than 0.05 were considered statistically significant. We conducted Pearson correlation analysis to test for relationships between personality traits. Because almost all the personality traits were correlated (see "Results"), we performed a factor analysis with varimax rotation of all eight personality traits. We identified three factors for further analyses as those showing eigenvalues greater than one. Hence, we identified and calculated the individual scores of each personality factor, and the relationships between individual personality scores and collective motion traits were tested by Pearson correlation analysis.

Results

Personality of individual fish

All variables associated with each personality trait (i.e., boldness, exploration, activity and sociability) were found to be highly correlated (Table 1). Furthermore, all variables associated with boldness, exploration and activity were correlated with one another, except that MDO was correlated only with PTM. The two sociability traits were not correlated with any of the variables except for one boldness variable, i.e., PTO.

The results of the factor analysis indicated that the eight variables could be reduced to three factors. The first factor explained 32.31% of the variance and was positively related to all boldness and activity variables; i.e., a higher score indicated higher boldness and activity (Table 2). The second factor explained 26.58% of the variance and was negatively related to sociability (negatively related to PTS and positively related to DTS) and PTO; i.e., a higher score indicated

Table 1 Pearson correlations between personality traits in the pale chub ($N=57$ for the two variables of boldness, $N=59$ for exploration and $N=60$ for all other variables; data are presented as the mean ± SE)

	Activity		Exploration		Boldness		Sociability	
	Median speed (cm s^{-1})	Percent time moving (%)	First time reaching the novel object (s)	Minimum distance to object (cm)	Number of inspections (time)	Percentage of time in open area (%)	Distance to shoal (cm)	Percentage of time with shoal (%)
Activity								
Median speed	5.60 ± 0.30	79.65 ± 2.18	202.5 ± 18.7	1.47 ± 0.11	28.67 ± 1.50	43.15 ± 2.20	9.08 ± 0.35	87.60 ± 1.02
Percent time moving		$R=0.854$ $P<0.001$	$R=-0.377$ $P=0.003$	$R=-0.200$ $P=0.128$	$R=0.580$ $P<0.001$	$R=-0.260$ $P=0.050$	$R=-0.223$ $P=0.090$	$R=0.184$ $P=0.164$
Exploration								
First time reaching the novel object			$R=-0.506$ $P<0.001$	$R=-0.359$ $P=0.005$	$R=0.539$ $P<0.001$	$R=0.342$ $P=0.009$	$R=-0.202$ $P=0.125$	$R=0.154$ $P=0.245$
Minimum distance to object				$R=0.598$ $P<0.001$	$R=-0.350$ $P=0.008$	$R=-0.318$ $P=0.016$	$R=0.026$ $P=0.847$	$R=0.033$ $P=0.806$
Boldness								
Number of inspections					$R=-0.246$ $P=0.065$	$R=-0.050$ $P=0.712$	$R=0.151$ $P=0.255$	$R=-0.103$ $P=0.439$
Percentage of time in open area						$R=0.615$ $P<0.001$	$R=0.052$ $P=0.703$	$R=-0.150$ $P=0.267$
Sociability								
Distance to shoal							$R=0.279$ $P=0.036$	$R=-0.255$ $P=0.056$
Percentage of time with shoal								$R=-0.834$ $P<0.001$

Table 2 Factor loadings from the personality measurements

	Boldness (32.31%)	Sociability (26.58%)	Exploration (20.69%)
Number of inspections	0.817		
Percentage of time in open area	0.640	0.469	
Median speed	0.844		
Percentage of time moving	0.817		
First time reaching the novel object			0.816
Minimum distance to object			0.921
Distance to stimulus shoal		0.924	
Percentage of time with shoal		-0.922	

Values listed in the table are those with final loadings above 0.40

lower sociability. The third factor explained 20.69% of the variance and was negatively related to the two variables associated with exploration; i.e., a higher score indicated less exploration.

Relationships between factor scores of personality traits and collective motion traits

The median speed, SS, DGC, SSA and body-turning rate were 8.91 ± 0.33 cm s^{-1}, 0.71 ± 0.01, 13.80 ± 0.41 cm, $0.67 \pm 0.01°$ and $0.06 \pm 0.0°$ s^{-1}, respectively. The first personality score was negatively correlated with SSA (Fig. 2a), whereas the second personality score was negatively correlated with SS (Fig. 2b). The third personality score was not correlated with any collective motion traits.

Discussion

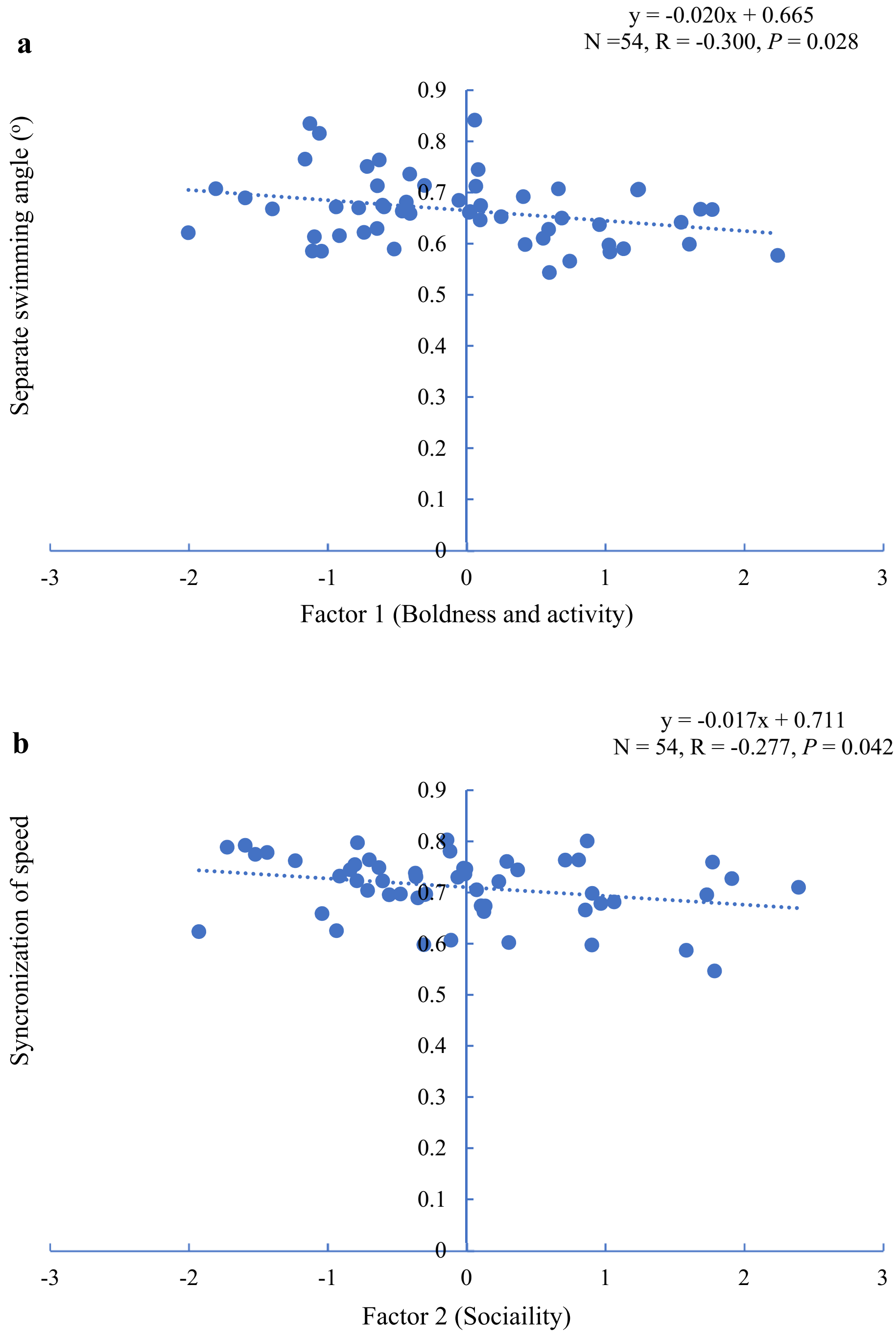
Personality of pale chubs

All personality traits were measured at the same time for more than 100 min, which is a long period of manipulation. This could be stressful for the fish, and individuals with different personalities might react differently to such stress. However, similar to in other fish species, most of the variables associated with boldness, exploration and activity were closely related in pale chub; i.e., the species exhibited behavioral syndromes (see review in Sih et al. 2004; Cote et al. 2010; Liu and Fu 2017). This relationship was reinforced by the results of the factor analysis, which showed that the variables related to boldness and activity could be reduced to one factor of personality. Furthermore, both variables associated with sociability exhibited significant correlations with one boldness variable, i.e., PTO. The relationship was again reinforced by the results of factor analysis in that the two sociability traits and PTO could be reduced to the sociability factor of personality. This might suggest that less sociable pale chub individuals are bolder than more sociable individuals. A previous study on mosquitofish (*Gambusia affinis*) also found that sociability was negatively correlated with boldness (Cote et al. 2013). Thus, it has been suggested that sociability is negatively correlated with boldness and/or exploration and that fish with high exploration tendencies are usually less sociable than those that are less likely to explore their environment (Jolles et al. 2017).

The relationship between personality and collective motion

The main aim of this study was to determine whether fish with different personalities display different movement characteristics when swimming in groups. It has long been suggested that synchronized collective movements occur when group members adjust their behaviors according to the movements and locations of their group mates, thus maintaining the cohesion of the group (Lukeman et al. 2010; Herbert-Read et al. 2011; Katz et al. 2011). However, withholding individuality in swimming behavior when in a group to some extent is also suggested to be advantageous (Couzin et al. 2011; Spiegel et al. 2017). In the present study, the first personality score (mostly related to boldness and activity) was negatively correlated with SSA. This result suggests that proactive individuals showed higher polarity with the group centroid, i.e., the same movement direction as that of the school. It has been suggested that alignment responses (low SSA indicates high alignment) appeared to be important in transferring information between group members and providing synergistic benefits to groups members (Sumpter et al. 2018). This correlation suggests that the personality of a pale chub is related to its movement traits, which has implications for fitness: for fish groups in a natural setting, proactive fish are highly polarized in swimming direction and can gain more synergistic benefits than reactive individuals. The correlation between PTO and DTS in the present study and the relationship between the boldness score and shoaling tendency in zebrafish (*Danio rerio*) also suggest that measures of personality, such as the boldness score, are related to

Fig. 2 Relationships between factor scores of personality traits according to factor analysis and collective motion traits in the pale chub



shoaling tendency in certain fish species (Way et al. 2015). Interestingly, a previous study in qingbo (*Spinibarbus sinensis*) found that swimming speed and its synchronization were driven more by less bold group members than by group members with higher boldness. This suggests that personality traits, such as boldness traits, must be maintained to some degree when an individual joins a group. Thus, the present study, along with our recent study on qingbo, suggests that variation in the composition of fish groups in terms of personality might be a vital cause of variation in group-level behavior, as already observed in insects (Pruitt et al. 2013). Variation in group movement patterns might have ecological implications and fitness consequences such as information transferring and predation avoidance, for group-living fish survival in habitats with changes in food availability and predation stress.

The personality score related to sociability traits showed a negative correlation with SS, suggesting that highly social individuals were more synchronized in swimming speed with other group members than less social individuals (a high score indicates low sociability), which is in line with our expectation. A previous study found that individuals of lower sociability occupying the periphery and front played a more important role in determining group movement (Jolles et al. 2017). Scientists have long suggested that sociability is closely related to exploration and dispersal tendency (Cote et al. 2010). The correlation between personality traits associated with sociability and group behavior might have vital ecological relevance, as a subgroup of individuals showing different sociability levels is very likely to exert different ecological influences than a random group. Fish individuals with high sociability and, hence, high synchronization of speed might also be at an advantage in efficient information transferring and in consensus collective motion (Krause and Ruxton 2002).

The personality score related to exploration showed no relationship with any variables of collective motion, which was unexpected. Because the two exploration variables are closely correlated with activity, these two variables might not be proper indicators of exploration in the pale chub. They might instead be a reflection of activity because more active individuals took less time to reach the so-called novel object and might have approached the novel object independent of exploratory movement as a result of routine activity. The traits of such routine activity might vanish due to compromise among groupmates to achieve synchronized collective motion (Tang and Fu 2019). As noted above, the synchronized collective motion might be crucial to information transferring and anti-predation success for shoal-living fish in the field (Krause and Ruxton 2002; Sumpter et al. 2018; Lloren et al. 2019).

In summary, we conducted comprehensive behavioral experiments on individual personalities in combination with the movement traits of each individual when in a group. Our results demonstrated that personality (mainly boldness and sociability) has a significant effect on the swimming traits of different individuals in the group. Proactive individuals showed greater alignment tendency, which might give them an advantage in efficient information transferring and allow them to gain more synergistic benefits of group living, such as anti-predation effects, than reactive individuals. The interconnection between personality and collective motion together with the high interindividual variation in personality and movement traits during collective movement might provide the preconditions necessary for the occurrence of fish schools with great diversity in group-level characteristics. These outcomes provide key insights that might explain the occurrence of flexible collective movement patterns across different ecological and social contexts.

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Compliance with ethical standards

Conflict of interest None.

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