Effects of habitat conditions on the boldness and sociability of wild-caught fish (*Zacco platypus*) along a river

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Abstract

Wild fish show consistent behavioral differences, e.g., personalities among populations, whereas the possible relationships between personality and environmental conditions have seldom been systemically examined. We aimed to test whether the personality of wild-caught fish was affected by the biotic (food resources and predation) and abiotic (temperature, dissolved oxygen level, and flow velocity) conditions of natural habitats. Six populations of pale chub (*Zacco platypus*) were sampled along a river longer than 1000 km, and environmental conditions and personality characteristics, such as boldness, activity, and sociability, were measured. Personality variables could be reduced to two factors by principal component analysis, boldness, and sociability factors, with the former factor having more variation among and within populations. Individuals from populations with higher food availability (plankton density) and flow velocity generally showed higher boldness factor scores, possibly due to the better energy status of higher food abundance or the low water transparency and hence decreased predation risk and fast-flow lifestyle of populations with higher water velocity populations. All populations showed high sociability as group-living species, which was positively correlated with only the phytoplankton biomass, possibly due to decreased intraspecific competition in habitats with abundant food resources. The correlations among personality variables were population-dependent, as individuals who moved more had a shorter distance to the stimulus shoal (i.e., increased shoaling tendency) within high-predation populations, whereas individuals who moved more spent less time in shoals within low-predation populations. The results suggest that alterations in habitat conditions can result in divergent natural selection that favors a particular personality; thus, human-induced alterations in habitat conditions may shape the personality of individual fish.

Keywords Pale chub · Personality · Environmental condition · Food resource · Behavioral syndrome

Introduction

The evolutionary and ecological relevance of animal personalities, i.e., consistent individual behavioral differences over time and in different contexts, has drawn much attention from behavioral ecologists in recent years (Réale et al. 2010; Sih et al. 2012; Killen et al. 2016a; Jolles et al. 2017; Lloren et al. 2019). Habitat environmental conditions vary greatly for fish species, and divergent natural selection (DNS) promotes the behavioral traits of populations to different adaptive peaks, hence generating and maintaining phenotypic

diversities (Langerhans 2009). Predation is among the most vital agents in the DNS of animal personality (Burns et al., 2016). For example, a study on mosquitofish (*Gambusia affinis*) found that sociability contributed significantly to the possibility of being consumed by predators (Brodin et al. 2019), whereas a study on roaches (*Rutilus rutilus*) found that boldness contributed significantly to the possibility of being consumed by predators (Blake et al. 2018). Subsequently, it was found that wild-caught mosquitofish (*Gambusia hubbsi*) and guppies (*Poecilia reticulata*) from low-predation populations were less sociable and more exploratory than their high-predation counterparts (Burns et al. 2016; Heinen-Kay et al. 2016). However, studies on another poeciliid fish (*Brachyrhaphis episcopi*) and Eurasian minnows (*Phoxinus phoxinus*) found the opposite, i.e., individuals from low-predation populations were shyer than those from high-predation populations (Archard and Braithwaite 2011a;

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Kortet et al. 2015). These inconsistent results showed that the effects of predation stress on personalities likely rely on other contextual conditions (e.g., food availability, temperature, and water velocity). Thus, a more detailed investigation is needed to clarify the possible mechanisms of predation-driven personality variations. Interestingly, the previous studies on wild-caught pale chub (*Zacco platypus*) from high-predation areas exhibited a shorter response latency to escape, but a higher maintenance metabolism than those of fish from low-predation areas along the Wujiang River (Fu et al. 2015a). Whether there are differences in the personalities among different populations of pale chubs and whether the possible differences are related to habitat predation pressure might yield very interesting results and contribute to the current understanding of the maintenance of personality in the wild.

In the field, animals need to maintain the delicate balance between energy intake and mortality risk according to their body energy reserves (Näslund and Johnsson 2016). Hence, animal personalities correlate with variations in internal state dynamics, and personality might be closely related to food availability within a habitat (Careau et al. 2008; Holtmann et al. 2017). Thus, it is strange that most indoor studies found that variation in food abundance (e.g., fed once vs twice per day for several weeks) showed no effect on the personality of juvenile fish species (McGhee and Travis 2011; Liu and Fu 2017). However, studies on brown trout (*Salmo trutta*) fry fed under high-food availability conditions showed higher activity, suggesting that experience in the early life stage might exhibit a more distinct effect on personality, while once developed, the personality of an individual is relatively insensitive to short-term variations in food resources (Näslund and Johnsson 2016). Moreover, under extreme conditions, such as food deprivation, juvenile fish, such as qingbo (*Spinibarbus sinensis*) and European sea bass (*Dicentrarchus labrax*) showed increased exploratory behavior and/or decreased social interest (Aimon et al. 2019; Wang et al. 2019). In addition, food availability likely interacts with predation risk and shapes the personality of fish (Chuard et al. 2018). The effect of food abundance on the development and maintenance of personality in the field can yield important results; however, field work has seldom been performed until now, which is possibly due to the technical difficulties involved in quantifying food availability in natural habitats.

Fish in the field show a complex personality regime that has vital fitness consequences. Environmental variation can lead to DNS that alternatively or consistently favors particular personalities in different environments (Heinen-Kay et al. 2016). Owing to the construction of water conservancy projects (e.g., the Three Gorges Dam in China and the Aswan Project in Egypt) and water eutrophication, anthropogenic environmental changes, such as changes in temperature, food

availability, and flow regimes, could modify evolutionary trajectories by favoring alternative personality types under a given set of conditions (Killen et al. 2016b). Thus, a better understanding of animal behavior divergence in response to different habitat conditions could be decisive in forecasting the effects of environmental change on fish populations (Killen et al. 2016b). The recent studies have found that habitat structure and water transparency might have profound effects on the fitness outcome of personality (Sommer-Trembo et al. 2017; Church and Grant 2018; Ehlman et al. 2019; Lichtenstein et al. 2019). Thus, the precise prediction of personality alterations in the currently changing world might be important for fishery risk assessments and invasive species management (Heinen-Kay et al. 2016; Hirsch et al. 2017; Geffroy et al. 2020). However, no such systematic investigation of the relationships between environmental conditions and personality has been conducted until now.

The main goal of this study is to test whether there are differences in personality and whether such differences are related to the predation regime (high vs. low pressure), food availability (biomass and density of phytoplankton and zooplankton), flow regime (water velocity), and some environmental conditions (temperature and dissolved oxygen level) of habitats of wild-caught pale chub along a river. We measured all personality traits under homogeneous laboratory conditions because phenotypic flexibility in behavior and potential confounding environmental effects may obscure any differences in personality. The pale chub is a small cyprinid widely distributed in East Asia. This species shows profound phenotypic variation in morphology, metabolic traits, and locomotion performance across different habitats (Johansson 2006; Fu et al. 2015a). This species usually inhabits mountainous streams with high flow velocities and might account for 90% of the local fish catch in some extreme scenarios; however, the species also shares relatively low-flowing stream habitats with other fish species and predators. The Wujiang River, with a length greater than 1000 km, is one of the largest tributaries of the Three Gorges Reservoir. The predator conditions, flow velocity and food availability vary drastically across different sections (Fu et al. 2013; Lu 2019). Many dams have been built along the river, and these hydroprojects have altered the original habitat conditions.

Materials and methods

Sampling sites and fish collection

Juvenile pale chubs from six populations [Wengxi (WX), Jinfoshan (JFS), Zhenxiang (ZX), Baima (BM), Hechangba (HCB) and Daozhen (DZ)] along the Wujiang River were collected from July to August 2017 (Fig. 1). The body sizes

Fig. 1 The location map of the sampling sites. I: Wengxi, II: Jinfoshan III: Zhenxiong IV: Baima V: Hechangba VI: Daozhen

of the collected fish, ecological parameters, and geographical information for all sampling sites are listed in Table 1, and the location of each site has been described in maps in the previous studies (Fu et al. 2013, 2015a; b). The water temperature, flow velocity, and dissolved oxygen level were measured three times daily at approximately 8:00 am, 12:00 am and 17:00 pm for three consecutive days at all sampling sites as described in the previous studies (e.g., Fu et al. 2013). The number of velocity samples measured in each river section varied from 6 to 9 based on the river width. The populations were classified as ‘low predation’ or ‘high predation’ based on the absence or presence of piscivorous fish, such as southern catfish (*Silurus meridionalis*), mandarin fish (*Siniperca kneri*), predatory carp (*Chanodichthys erythropterus*), and Chinese catfish (*Silurus asotus*), which were determined by interview surveys with local fishermen, observing, and recording the abundance of predators according to the local fishery catch data from the most recent 5 days and the results of our previous studies (Fu et al. 2013, 2015a; b). Among the six sites, we collected several southern catfish and Chinese catfish at three sites (BM, HCB, and DZ), and the local fishermen frequently collected piscivorous fish, such as southern catfish and other predators

frequently. However, at the remaining three sites, we did not collect any natural predators of pale chub during the sampling time, and none of these predators except a few Chinese catfish were caught by fishermen. Thus, the former three sites (BM, HCB, and DZ) were classified as high-predation sites, and the remaining three sites (WX, JFS, and ZX) were low-predation sites.

The fishing gear used for pale chub was the casting-net shrimp trap. The trap is a cylinder net (diameter of 40 cm and height of 60 cm) with four holes made from a wing net around the trap. The food item was put inside the trap as bait. The fish can move into the trap, but usually cannot move out due to the structure of the hole. We collected juvenile pale chubs with a standard body length of less than 10 cm and released others directly back into the collection sites. We used this collection method because it causes negligible harm and stress to the collected samples and other fish individuals who were released to the field as compared to other methods, such as fishing and gill nets. Furthermore, this collection method might also have little sampling bias that could influence the outcomes of personality measurements as compared to other collection methods (Härkönen et al. 2014). We transferred the collected samples to the

Table 1 Summary of the collection sites and ecological parameters

Collection sites	Wengxi (WX)	Jinfoshan (JFS)	Zhenxiong (ZX)	Baima (BM)	Hechangba (HCB)	Daozhen (DZ)
Predation stress	Low	Low	Low	High	High	High
Coordinates	N27°51'82" E108°22'98"	N29°06'52" E107°13'19"	N27°23'29" E104°53'52"	N29°24'37" E107°31'55"	N27°37'26" E108°01'34"	N29°02'32" E107°31'55"
Dissolved oxygen level (% saturation)	108.88 ± 3.10 ^{bc}	104.85 ± 11.44 ^{cd}	82.44 ± 0.35 ^f	101.47 ± 0.07 ^d	126.75 ± 0.38 ^a	91.08 ± 0.15 ^e
Water temperature (°C)	29.07 ± 0.03 ^a	27.30 ± 0.12 ^c	21.70 ± 0.06 ^f	25.60 ± 0.10 ^e	28.73 ± 0.13 ^b	26.23 ± 0.09 ^d
Flow velocity (cm s ⁻¹)	44.97 ± 9.52	59.47 ± 11.44	26.20 ± 8.54	54.67 ± 14.22	31.96 ± 9.56	44.70 ± 10.66
Body mass (g)	2.12 ± 0.08 ^c	2.10 ± 0.11 ^{cd}	1.72 ± 0.18 ^d	3.24 ± 0.20 ^b	5.38 ± 0.28 ^a	2.55 ± 0.15 ^c
Body length (cm)	5.45 ± 0.07 ^{cd}	5.32 ± 0.07 ^{cd}	5.09 ± 0.12 ^d	6.04 ± 0.12 ^b	7.08 ± 0.12 ^a	5.62 ± 0.10 ^c
Phytoplankton						
Biomass (mg L ⁻¹)	2.834E-1	2.120E-2	1.849E-10	1.167E-1	1.550E-4	1.568E-1
Density (no L ⁻¹)	1.150E+10	6.229E+9	4.200E+2	1.642E+10	7.470E+9	8.720E+10
Zooplankton						
Biomass (mg L ⁻¹)	2.109E-3	7.030E-4	1.920E-3	7.138E-3	2.472E-3	1.524E-3
Density (no L ⁻¹)	4.360E+9	3.737E+9	1.401E+9	6.229E+9	1.401E+9	8.097E+9

N = 3 for the dissolved oxygen level, water temperature and water velocity, and *N* = 20 for the body mass and body length; see details in the Methods and Materials section

The comparison of all ecological parameters of six sample sites was performed by one-way ANOVA, followed by Duncan's post hoc test. a, b, c, and d values not sharing the same letter indicate significant differences at *P* < 0.05

laboratory and maintained the fish from each population in a thermoregulated tank (250 L), gradually adjusting the water temperature from the local temperature to a standard temperature (25 ± 1 °C) (the temperature was increased or decreased by 2 °C per day). Each population was held in their own unique 250 L tank to avoid mixing and misidentification, and at least one quarter of the water in the tank was refreshed daily. The photoperiod was maintained as a 12 h light:12 h dark cycle. The fish were fed to apparent satiation once daily (at 8:30 am) for 15 days with *Tubifex* worms after temperature stabilization. The uneaten food and feces were cleaned by a siphon at 9:30 am. The water oxygen tension was kept above 90% saturation.

Ethical note

This study was approved by the Animal Care and Use Committee of the Key Laboratory of Animal Biology of Chongqing (permit number Zhao-20170324-01) and performed in strict accordance with the recommendations of the Guide for the Care and Use of Animals at the Key Laboratory of Animal Biology of Chongqing, China. All fish were returned to the collection sites once the experiment was finished.

Collection of water samples and measurement of water plankton

The water samples for phytoplankton analysis consisted of 1 L of water sampled by a water sampler and fixed with 1% Lugol for later analysis. The water samples for zooplankton

analysis totaled 10–50 L and were filtered by a mesh net (64 µm) and then fixed with Lugol for later analysis. The phytoplankton, protozoa, rotifers, and cladocerans (or copepods) were counted in 0.1 mL, 0.1 mL, 1 mL and 5 mL plankton counting chambers via microscopy, respectively. The biomass was calculated by the model selected by the AlgaeC intelligent identification system for plankton count analysis (Tan et al. 2017). All assays were carried out in duplicate, and the average values were used for further analysis.

Experimental apparatus and protocol

Personality variables, including the boldness, activity, and sociability of all fish were measured. The measurements were conducted in aquaria from 8:00 am to 17:00 pm. The test fish were quickly transferred into aquaria in another experimental room in a small bucket containing water from the home tank (approximately 3 min). The water temperature of the experimental aquaria was maintained at 25 ± 2 °C, and the aquaria were washed after each measurement. We tested the behavior of fish from JFS and BM first, then HK and WX, and finally, WX and HCB, which was according to the order the field fish were transferred into the laboratory. The fish were deprived of the food on the testing day. All the measurements were conducted twice over 2 consecutive days, and the means were used for data analysis.

A rectangular tank (length × width × height: 70 × 35 × 35 cm) was used as the aquarium to measure the personality variables of boldness and activity. The aquarium was separated into a shelter partition

(length $\times$ width $\times$ height: 15 $\times$ 35 $\times$ 35 cm) and an open partition (length $\times$ width $\times$ height: 55 $\times$ 35 $\times$ 35 cm) by white opaque partition. A diagram of the structure of the aquarium was presented in a previous study (Liu and Fu 2017). A webcam was located directly above the aquarium to record the behaviors. Four aquaria were used to test the boldness and activity at the same time. Briefly, a test fish was transferred into the shelter partition of an aquarium and allowed to preacclimate for 0.5 h for the measurement of boldness. Then, the small door between the shelter and open partitions was gently opened, and the behavior of the test fish was videotaped for 0.5 h at 15 frames s^{-1} . The number of inspections (NOI), i.e., the total number of test fish entering the open area and the percentage of time in the open area (PTO), were used as indicators of boldness. If a test fish exhibited a relatively high NOI (or PTO), it was considered as a bolder individual. After the measurement of boldness, the test fish were kept in the open area, but the door between the open and shelter partitions was closed. The behavior of the test fish was videotaped for another 10 min. The percentage of time spent moving (PTM) and the total distance moved (TDM) were used to measure the activity. If the fish showed a relatively high PTM and a relatively high TDM, it was considered a more active individual. The aquarium was cleaned and exchanged with freshwater after each measurement.

Sociability was recorded using a rectangular aquarium (i.e., 70 $\times$ 35 $\times$ 35 cm). The aquarium was separated into two stimulus subareas (15 $\times$ 35 $\times$ 35 cm) on both sides and a test subarea in the middle (40 $\times$ 35 $\times$ 35 cm) by two transparent partitions. Structural diagrams of the aquarium were presented in the previous studies (Killen et al., 2016a; Bai et al., 2018). Sociability was measured in four identical aquariums immediately after the recording of activity. Six stimulus individuals from the same home tank and habitat with the test fish were first moved to the stimulus subarea (alternating between the right and left areas), and then after 5 min, the test fish was rapidly moved to the test subarea using a small bucket (approximately 1 min), where the movement of the test fish was videotaped for 15 min. The aquarium was cleaned and exchanged with freshwater, and new stimulus individuals were transferred to the aquarium after each measurement. The stimulus individuals were used repeatedly due to the limitation of the number of fish, but the stimulus fish were not used in two consecutive tests. The percentage of time that the test individuals stayed within 20 cm of the stimulus subarea (PTS) and the mean distance to the stimulus shoal (DTS) were used as indicators of sociability (Miller & Gerlai, 2012; Killen et al. 2016a). If a fish showed a relatively high PTS and a short DTS, it was considered a more sociable fish.

The videos were converted from.wmv to.avi format (Format Factory, <http://format-factory.softonic.cn>), and 5 videos (2 videos of the boldness test from JFS and 3 videos of the

sociability, including 1 from WX and 2 from JFS) failed to be converted and were excluded from further analysis (see details in Supp. Table 1). Then, the coordinates of the test individual were extracted by idTracker (V 2.1) (Pérez-Escudero et al. 2014). The PTM was calculated as the percentage of time that the swimming speed was higher than 1.75 $cm\ s^{-1}$ throughout the duration of observation (i.e., 10 min), while the swimming 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 measured fish at time t and those at the time of the previous frame ($t-1$), respectively, and d is the time interval between two frames. The TDM was the total distance moved by the test fish over the whole measurement period of activity (10 min). The DTS indicating sociability was the mean distance of the test fish from the partition between the test and stimulus areas over the whole measurement period (15 min). The NOI indicating boldness, i.e., the number of inspections in the open area of the aquarium, was counted as the number of segments of the consecutive coordinates of the experimental fish. The coordinates of the test fish could only be detected when the test fish entered the open area because the activities of the experimental fish in the shelter area were not videotaped, and the coordinates in the shelter area could not be detected. The PTO was determined by the ratio of the frames with the test fish in the open area to the total frames over the whole 15 min boldness observation [i.e., 13,500 frames (15 frame $s^{-1} \times 60\ s \times 15$)].

Data analysis

SPSS 17 was used for data analysis. The data are shown as the means $\pm$ standard errors, and P values less than or equal to 0.05 were considered statistically significant. We ran a principal component analysis (PCA) with varimax rotation on six personality variables, which reduced the correlated measures of the personality tests (boldness, activity, and sociability tests, including 6 variables—percentage of time in the open area, number of inspections, percentage of time moving, total distance moved, distance to shoal, and percentage of time with the stimulus shoal) to principal components. Two factors (i.e., hereafter referred to as the “boldness factor” and “sociability factor”) with eigenvalues greater than 1 were identified for further analyses. The factors were subjected to orthogonal (varimax) rotation, which is suggested for smaller sample sizes and to aid in the interpretation of factor loadings. Then, the scores of each personality factor were extracted using the linear regression method. We conducted multiple linear regression to evaluate the effects of biotic (predator and food abundance) and abiotic (water

Table 2 Loadings of the two factors extracted by principal component analysis (PCA) of personality measurements

	Factor 1 (Boldness factor) (40.46%)	Factor 2 (Sociability factor) (29.33%)
Percentage of time in open area (PTO)	0.600	
Number of inspections (NOI)	0.686	
Percentage of time moving (PTM)	0.917	
Total distance moved (TDM)	0.859	
Distance to shoal (DTS)		– 0.930
Percentage of time with the shoal (PTS)		0.938

Only loading values above 0.4 are listed. Values in parentheses are the proportions of total variation explained by each factor

temperature, water velocity, and dissolved oxygen level) factors on personalities.

Results

The personality traits of pale chubs

Pale chubs showed large variations in personality traits related to boldness and activity at both the interpopulation and intrapopulation (indicated by CV values in the parentheses) levels (Supp. Table 1). However, all populations showed high sociability with relatively less variation (all populations showed PTS values higher than 87% with DTS values shorter than 1 body length). The factor analysis showed that all six variables could be reduced to two factors (Table 2). The first factor explained 40.46% of the variance and was positively related to all boldness and activity variables, i.e., a higher score implied a proactive personality (bolder, more explorative, and aggressive characteristics). The second factor explained 29.33% of the variance and was positively related to sociability (negatively related to the distance to the stimulus shoal and positively related to the percentage of time in the preference zone), i.e., a higher score implied higher sociability.

Effect of biotic parameters on personality

Multiple linear regression analysis indicated that predation had no significant correlation with either personality factor score (Table 3). The densities of both phytoplankton and zooplankton were positively correlated with boldness scores (Fig. 2). Furthermore, the biomass of phytoplankton was negatively correlated with boldness scores, but positively correlated with sociability scores.

Effect of abiotic parameters on personality

Multiple regression analysis indicated that the water temperature and sampling site had no significant relationship

Table 3 The results of multiple regression analysis of the effects of ecological biotic factors on personality

	Boldness score	Sociability score
Overall F test	$F = 10.733$ $P < 0.001^*$	$F = 18.257$ $P < 0.001^*$
Body mass	Slope = – 0.070 $t = -0.663$ $P = 0.508$	Slope = – 0.073 $t = -0.797$ $P = 0.427$
Abundance of predator	Slope = – 0.128 $t = -1.005$ $P = 0.317$	Slope = – 0.081 $t = -0.916$ $P = 0.362$
Phytoplankton density	Slope = 5.43E-11 $t = 2.418$ $P = 0.017^*$	Slope = 0.060 $t = 0.058$ $P = 0.954$
Phytoplankton biomass	Slope = – 4.123 $t = -3.824$ $P < 0.001^*$	Slope = 3.631 $t = 4.273$ $P < 0.001^*$
Zooplankton density	Slope = 1.38E-10 $t = 3.573$ $P = 0.001^*$	Slope = – 0.085 $t = -0.773$ $P = 0.441$
Zooplankton biomass	Slope = – 0.235 $t = -1.631$ $P = 0.106$	Slope = 0.055 $t = 0.622$ $P = 0.535$

* $P < 0.05$

with either personality factor score (Table 4). The dissolved oxygen level was significantly correlated with sociability scores, but not with boldness scores. In contrast, the water flow velocity was not correlated with the sociability scores, but positively correlated with the boldness scores.

Correlations between personality variables within each predation regime

The correlations among the six personality variables indicated that the relationships were predation dependent. When analyzed among all six populations, all boldness and activity variables were significantly correlated with each other, whereas sociability variables were correlated with each other

Fig. 2 The relationship between personality scores and some environmental parameters ($N = 113$)

Table 4 The results of multiple regression analysis of the effects of ecological abiotic factors on personality

	Boldness score	Sociability score
Overall F test	$F = 31.710$ $P < 0.001^*$	$F = 6.363$ $P = 0.002^*$
Body mass	Slope = -0.770 $t = -0.896$ $P = 0.327$	Slope = -0.147 $t = -2.381$ $P = 0.019^*$
Water velocity	Slope = 3.930 $t = 5.631$ $P < 0.001^*$	Slope = -0.067 $t = -0.721$ $P = 0.472$
Water temperature	Slope = -0.054 $t = -0.598$ $P = 0.551$	Slope = -0.221 $t = -1.287$ $P = 0.201$
Dissolved oxygen level	Slope = -0.082 $t = -0.947$ $P = 0.332$	Slope = 1.999 $t = 3.076$ $P = 0.003$
Sample sites	Slope = -0.163 $t = -1.390$ $P = 0.167$	Slope = 0.053 $t = 0.542$ $P = 0.589$

* $P < 0.05$

but showed no relationship with any boldness or activity variables (Table 5). When analyzed within low-predation populations, two activity variables were negatively correlated with PTS, whereas these relationships disappeared within high-predation populations (Fig. 3). When analyzed within high-predation populations, two activity variables were negatively correlated with DTS, while these relationships did not exist within low-predation populations.

Discussion

The present study conducted a systematic investigation of the relationships between biotic and abiotic habitat conditions and personality in wild-caught pale chubs. In contrast to expectation, we found that predation showed no correlation with boldness scores or sociability scores, which might have been masked or altered by environmental factors, such as water velocity and food resources. As anticipated, fish in habitats with abundant food resources usually have high boldness and sociability scores, possibly due to good body conditions and lower levels of interindividual competition. Water velocity showed a profound positive effect on the boldness scores, which might be due to the low water transparency and hence decreased predation risk for pale chubs in fast-flow habitats. The relationship between sociability variables and activity variables was population dependent, as it changed from either a negative relationship or no significant correlation in low-predation populations to no

Table 5 Spearman's correlation results among personality traits in all populations and within high- and low-predation populations (N =varied from 113 to 119, from 59 to 60 and from 55 to 60, respectively) and the correlation index (R) and significance (P) are presented

	Percentage of time in open area	Number of inspections	Percentage of time moving	Distance moved	Distance to shoal	Percentage of time with shoal
Six populations						
Percentage of time in open area		$R=0.554$ $P<0.001^*$	$R=0.364$ $P<0.001^*$	$R=0.239$ $P=0.009^*$	$R=0.018$ $P=0.854$	$R=-0.107$ $P=0.259$
Number of inspections			$R=0.442$ $P<0.001^*$	$R=0.365$ $P<0.001^*$	$R=-0.042$ $P=0.659$	$R=-0.021$ $P=0.827$
Percentage of time moving				$R=0.912$ $P<0.001^*$	$R=-0.035$ $P=0.709$	$R=-0.134$ $P=0.154$
Distance moved					$R=-0.051$ $P=0.585$	$R=-0.077$ $P=0.412$
Distance to shoal						$R=-0.781$ $P<0.001^*$
Percentage of time with shoal						
Low predation population						
Percentage of time in open area		$R=0.645$ $P<0.001^*$	$R=0.345$ $P=0.008^*$	$R=0.220$ $P=0.096$	$R=-0.014$ $P=0.920$	$R=-0.057$ $P=0.681$
Number of inspections			$R=0.404$ $P=0.002^*$	$R=0.374$ $P=0.004^*$	$R=-0.064$ $P=0.641$	$R=-0.057$ $P=0.681$
Percentage of time moving				$R=0.901$ $P<0.001^*$	$R=0.112$ $P=0.408$	$R=-0.303$ $P=0.022^*$
Distance moved					$R=0.154$ $P=0.252$	$R=-0.273$ $P=0.040^*$
Distance to shoal						$R=-0.732$ $P<0.001^*$
Percentage of time with shoal						
High predation population						
Percentage of time in open area		$R=0.424$ $P=0.001^*$	$R=0.267$ $P=0.041^*$	$R=0.208$ $P=0.113$	$R=-0.135$ $P=0.313$	$R=0.181$ $P=0.175$
Number of inspections			$R=0.421$ $P=0.001^*$	$R=0.334$ $P=0.010^*$	$R=-0.146$ $P=0.275$	$R=0.170$ $P=0.202$
Percentage of time moving				$R=0.942$ $P<0.001^*$	$R=-0.278$ $P=0.035^*$	$R=0.159$ $P=0.233$
Distance moved					$R=-0.324$ $P=0.013^*$	$R=0.185$ $P=0.164$
Distance to shoal						$R=-0.812$ $P<0.001^*$
Percentage of time with shoal						

*Indicates a significant difference at the level of $P<0.05$

significant correlation or a positive relationship in high-predation populations.

Effects of predation and food resources on personalities among pale chub populations

The present study found that the boldness scores of individuals had no correlation with predation. However, in the same species, our previous findings showed that although boldness traits (the time spent in the shelter and latency to emerge) showed no significant difference between high- and low-predation populations, the activity (distance moved during

20 min of measurement) and risk-taking behavior (time spent in the risk area) of the high-predation populations were significantly lower than those of the low-predation regimes (Fu et al. 2015a; b). This disagreement between the two studies is likely due to the different analysis methods applied. Because the complicated interactive effects of environmental factors and predation make the situation unpredictable, the direction of the predation effect might be masked or altered by environmental factors, such as the water velocity and food resources. In the current study, we considered all biotic factors in the analysis model, while a previous study only focused on the predation stress and

Fig. 3 The relationships between the activity variables and sociability variables within either high-predation populations (filled circle) or low-predation populations

ignored the food abundance effects. This conclusion can be further supported by the fact that the antipredator behaviors involved in the swimming performance of pale chubs, such as the response latency, turning radius, and the maximum linear velocity ($V_{\max}$), also presented no correlation with the abundance of predators using multiple aggression analysis (Fu et al. 2013). In addition, it was found in poeciliid fish (e.g., *B. episcopi*) fish and Eurasian minnows that high-predation populations were more active or generally bolder than low-predation populations (Archard and Braithwaite 2011b; Kortet et al. 2015). However, wild-caught guppies and Bahamian mosquitofish collected from low-risk areas exhibited more exploratory activities than those from high-risk areas due to the high fitness costs of risk-taking behavior in high-predation habitats (Burns et al., 2016; Heinen-Kay et al. 2016). The inconsistency among species indicates the need for further investigation.

This study demonstrated no relationship between sociability and predation stress, possibly due to the high shoaling tendency of pale chubs, as fish from all populations had low DTS (less than 0.9 body length) and high PTS values with little variation. A previous study of collective-living cyprinid species, such as grass carp (*Ctenopharyngodon idellus*) and qingbo found that the DTS values varied from approximately 1.2–1.5 times the body length and that the PTS values were more than 80% (Killen et al. 2016a; Bai et al. 2018). It has long been suggested that group living has great ecological benefits, including defense against predators (due to the so-called confusion effect, dilution effect and many-eye effect) and improved swimming efficiency (Hemelrijk et al. 2015). Thus, staying in high-cohesion groups is vitally important for small fish species, such as pale chubs living in habitats with fast flows.

Interestingly, we found that the correlations between personality traits are predation–pressure-dependent. When examining correlations within low-predation populations, we found that both activity variables were negatively correlated with the PTS. However, these relationships disappeared, and negative correlations between the two activity variables and the DTS (please note that larger DTS values indicate less sociability) was found in pale chubs from three high-predation populations. This result suggests that the correlations between sociability and activity were plastic, as the DTS varied from a lack of significant correlation to a positive correlation while the PTS varied from a negative correlation to a lack of significant correlation with the increase in predation pressure. The negative relationship between activity and sociability has long been suggested as a concept of behavioral syndrome, as individuals exhibit more exploratory or other risk-taking behavior, usually with less cohesion, and spend more time at the edge of the group (Jolles et al. 2017). However, the mechanism of the positive relationship between activity and sociability

in high-predation habitats is difficult to explain. It is worth noting that studies on three-spined stickleback (*Gasterosteus aculeatus*), Egyptian mouthbreeder (*Pseudocrenilabrus multicolor*) and a neotropical poeciliid (*Poecilia vivipara*) also found that the correlations between different personality traits were population-dependent (Dingemanse et al. 2007; Sommer-Trembo et al. 2017; Oldham et al. 2019). It has been suggested that such inconsistencies in correlation results might be due to the adaptive behavioral adjustments of neophobia to variations in predation pressure and (or) consequent changes in intraspecific competition (competition usually increases with decreased predation pressure) (Sommer-Trembo et al. 2017; Sadoul et al. 2021). The mean boldness scores of high-predation populations increased as compared to those of the low-predation populations (except in JFS due to the very high-water velocity within the habitat, as mentioned previously), and this result might be because proactive individuals in the high-predation population showed suppressed neophobia and upregulated foraging and inspection behaviors. These fish use other coevolved adaptations, such as high sociability and hence high cohesion during shoaling, as antipredation strategies. It has been frequently found that some pale chubs hide behind or under tree roots and rock crevices in fast-flowing water, and these individuals might show less activity and have a lower shoaling tendency. Thus, the continuum between active with high cohesion and inactive and solitary individuals in high-predation habitats resulted in an unusually positive correlation, whereas such a correlation did not exist in low-predation habitats due to the increased intraspecific competition for food resources.

The scores of boldness factors showed positive correlations with the phytoplankton and zooplankton density. This is the first study to examine the relationship between personality traits and food resources in the field. The positive correlation between the food abundance (phytoplankton and zooplankton densities) and boldness score was anticipated, as individuals in habitats with high food availability are more likely to have good body conditions and be more active and bolder (Näslund and Johnsson 2016). It is also reasonable to observe that pale chubs from habitats with high phytoplankton biomass showed high sociability, as less intraspecific competition occurs as the amount of food resources increases. However, the zooplankton biomass showed no relationship with either factor score, and the phytoplankton biomass showed a negative correlation with the boldness score. The possible reason might be that some plankton species were too large to be prey for pale chub. Because most laboratory studies using juveniles as experimental models failed to find a relationship between food resources and personality, the present study suggested that the personality of some fish species might develop in some key early life-history

stages, and similar patterns may be demonstrated in coping behaviors (Langenhof and Komdeur, 2018).

The effects of the flow velocity and other abiotic conditions on personality

This study tested the influence of the water velocity on personality in fish and demonstrated that the water flow velocity had an intense influence on the boldness scores. Previous studies found that pale chubs from habitats with high water velocities showed strong swimming performance (both bursting and sustainable swimming speed), a high maintenance metabolism and elevated vigilance (Fu et al. 2013, 2015a). These results might suggest that fish populations from habitats with high water velocities exhibit a lifestyle characterized by fast pace-of-life syndrome (POLS), possibly due to the highly energy-demanding situation (Yan et al. 2013; Montiglio et al. 2018; Pang et al. 2020). These fish may be at greater risk of experiencing an energy deficit when the food abundance is low. In addition to the energy-demanding nature of high-velocity habitats, other physical conditions might be involved in shaping personality. For example, as compared to low and high turbidity (0 and 40 nephelometric turbidity units, 0 and 40 NTU), intermediate turbidity (20 NTU) elicited the greatest antipredator response, with activity and exploration diminishing to the greatest extent and, generated repeatable behavior in mosquitofish (*Gambusia affinis*) (Ehlman et al. 2019). This suggests that abiotic factors, such as the water transparency (turbidity) play vital roles in personality development (Sommer-Trembo et al. 2017; Ehlman et al. 2019). Sampling sites with high water velocities usually had low transparencies, which may make it more difficult for predators to detect prey, thus putting less pressure on more active individuals (similar to a habitat with high turbidity). Because the water flow velocity changed profoundly in the Wujiang River in the recent decades due to habitat alterations, it is possible that manmade environmental alterations may shape the personalities of individuals by interacting with the predation risk (Ehlman et al. 2019).

The present study found that the water temperature did not show any relationship with personality. However, the finding that the dissolved oxygen level showed no relationship with boldness scores, but was positively correlated with sociability scores was unexpected. The reason for this result might be that populations in habitats with high dissolved oxygen levels usually have abundant food resources, and the latter was positively correlated with sociability scores.

Conclusion

The present study found that both biotic factors, such as food resources, and abiotic factors, such as flow velocity, have profound effects on personality in different fish populations. Generally, pale chubs are more proactive with increases in flow velocity and food abundance. As a collective-living species, all pale chub populations showed high sociability with low variation, and sociability was only positively correlated with food resources (phytoplankton biomass). Furthermore, the present study found that the relationships between different personality traits were predation dependent. These results demonstrated that personality traits are profoundly affected by ecological factors; hence, environmental change can result in DNS that favors particular behaviors. The present study also suggests that when investigating the development and maintenance of personality in wild fish, abiotic factors, especially the flow regime, should receive increased attention, and some detailed information, such as the foraging modes of predators, might also be considered in the future.

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Declarations

Conflict of interest None.

Ethical approval This study complied with the current law of the country in which it was performed and was approved by the Animal Care and Use Committee of the Key Laboratory of Animal Biology of Chongqing (Permit Number: Zhao-20151010-01). The study was performed in strict accordance with the recommendations in the Guide for the Care and Use of Animals at the Key Laboratory of Animal Biology of Chongqing, China. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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