Current Zoology, 2021, 67(5), 481–488
doi: 10.1093/cz/zoab003
Advance Access Publication Date: 20 January 2021
Article

Article

Environmental temperature during early life affects the personality of mosquitofish in adulthood

Haifeng Li[a], Xinyu Zhang[a], Yi Wu[b], Feng Zhang[a], and Chunlin Li [a,*]

[a]School of Resources and Environmental Engineering, Anhui University, Hefei 230601, China and [b]Ministry of Ecology and Environment, Nanjing Institute of Environmental Sciences, Nanjing 210042, China

*Address correspondence to Chunlin Li. E-mail: lichunlin1985@163.com.

Handling editor: Claudio Carere

Received on 15 November 2020; accepted on 8 January 2021

Abstract

Personality has been observed in a variety of animal taxa with important implications in ecology and evolution. Exploring the influence of environmental temperature during early life on personality could help to understand the ontogeny of this phenotypic trait in animals. In this study, we reared newborn mosquitofish *Gambusia affinis* at high (30°C) and low (25°C) water temperatures and measured their shyness and exploration upon sexual maturity. We tested the repeatability of each behavioral trait; the correlation between them; and the effects of rearing temperature, sex, and body length on the behaviors. When growing up at low temperatures, female fish exhibited repeatability in shyness and exploration, and males exhibited marginal repeatability in shyness. However, neither of the 2 behaviors were repeatable when the fish were reared at high temperatures. There was a negative correlation between shyness and exploration, indicating that the 2 behaviors comprise a behavioral syndrome in this species. Mosquitofish reared at high temperatures were more explorative than those reared at low temperatures, while there was no difference in shyness between the 2 treatments. Body length and sex had no significant effects on the average values of the 2 behaviors. The results indicate that environmental temperature during early life could shape the personality of mosquitofish and modify the average of the behavioral traits. These findings might provide insights to understand the ontogeny of animal personality and how changes in environmental temperature influence animal dispersal by shaping their personality.

Key words: behavioral consistency, behavioral syndromes, boldness, exploration, repeatability, shyness

Animal personality refers to repeatable between-individual differences and within-individual consistency in behaviors over time and/or across contexts, contributing an important component to intraspecific variations in populations (Briffa and Weiss 2010; Dingemanse et al. 2010). A large body of evidence supports that a wide variety of vertebrates and invertebrates exhibit personality, which has been attracting increasing theoretical and empirical research attention (Sih et al. 2004). The existence of personality implies that behavioral plasticity is more limited than previously thought, and this may have important ecological and evolutionary implications, mainly because of the impact of personality on animals' fitness (Dingemanse and Réale 2005; Wolf and Weissing 2012). Quantifying animal personality and exploring the factors that shape its pattern may help to understand the mechanisms underlying inter-individual behavioral differences within populations and their implications in ecology and evolution (Réale et al. 2007).

Although animal behaviors have complex genetic bases, they might be strongly shaped by environmental factors, even more so than morphological traits (Dingemanse et al. 2010; Jolles et al. 2017). Living in different environments, animals may exhibit different personality types and adopt different behavioral strategies to cope with various environmental conditions (Bierbach et al. 2017). For example, fish in open habitats are bolder and more explorative than those in complex habitats (Dammhahn and Almeling 2012; Pearish et al. 2013). There are a variety of external and internal factors, such as food availability (Carere et al. 2005), predation risks (Bell and Sih 2007), body size (Polverino et al. 2016), and sex (King et al. 2013) that could shape animal personality with temporary or permanent effects. Animals are highly sensitive to environmental changes and the resultant modifications in behaviors may lead to changes in their fitness (Hoffmann and Sgro 2011). Although numerous studies have documented how animals behaviorally respond to environmental changes (Dingemanse and Réale 2005; Biro et al. 2010), empirical studies on how environmental factors shape personality along with animals' ontogeny are scarce.

Temperature is one of the most common environmental factors experienced by animals with significant effects on their growth and behaviors (Briffa et al. 2013). Changes in temperature can greatly influence animals' fitness, which may occur through various underlying mechanisms, such as changes in metabolic processes (Killen et al. 2010), foraging strategies (Castillo-Guerrero et al. 2016), and space use (Kvingedal and Einum 2011). Temperature may also influence animals' fitness by shaping their personalities. For example, a temperature increase might result in higher levels of activity, boldness, or aggression, leading to a rapid pace of life with fast growth and tendency to experience danger (Biro et al. 2010; Cavallo et al. 2015). More active and bolder individuals are more likely to have reproductive success, while shyer individuals may have greater survival rates (Smith and Blumstein 2008). In the context of global warming, exploring the effect of temperature on personality may help to understand how animals cope with changes in environmental temperature by modifying their personalities.

The influence of environmental factors on animals' behavior can occur throughout their lives, with different effects between sexes and among ontogenic stages (Langenhof et al. 2016). Special attention is suggested to be focused on the "sensitive windows" that are often present in animals' early growth (Fawcett and Frankenhuis 2015). The environment that animals experience in early life might affect both their morphological and behavioral phenotypes, which would have long-lasting effects on their adult lives (Garduno-Paz et al. 2010). For example, exposure to predation risk during early life can affect the growth of 3-spined stickleback *Gasterosteus aculeatus*, resulting in smaller body size in adulthood (Bell et al. 2011). As one of the behavioral phenotypes, adult personality can be consolidated and shaped by the environmental factors experienced during early life stages (Langenhof et al. 2016; Amat et al. 2018). Therefore, investigating the influence of environmental temperature during early life on personality may provide important insights into the ontogeny of this phenotypic trait (Killen et al. 2010; Gracceva et al. 2011).

In this study, we tested the effects of environmental temperature during early life on adulthood personality in mosquitofish *Gambusia affinis*. Mosquitofish is native to North America and has been intentionally introduced to many habitats worldwide with the initial aim of controlling mosquitos (Pyke 2008). Due to their notable tolerance to harsh environmental conditions and their global introduction, mosquitofish is considered the most widespread freshwater fish in the world (Garcia-Berthou et al. 2005). Affected by global warming, mosquitofish might adopt a rapid pace of life, that is, bolder and more explorative, which may facilitate their invasions. Here, we reared newborn mosquitofish at high and low temperatures and measured their personality traits, including shyness and exploration, upon sexual maturity. We quantified the repeatability of the 2 behavioral traits and their correlation and then tested the effects of rearing temperature, sex, and body length on the mean behavioral levels. We expected that shyness and exploration would be repeatable (i.e., personality), and that the 2 behaviors would be correlated (i.e., behavioral syndrome). We also expected that the fish reared at high temperatures would be bolder and more explorative than those reared at low temperatures.

Materials and Methods

Study animals and rearing conditions

Mosquitofish is a freshwater fish species of the family Poeciliidae of the order Cyprinodontiformes. It feeds on zooplankton, small insects, and insect larvae and gets its common name from its diet, which contains large number of mosquito larvae. Mosquitofish is characterized by internal fertilization and ovoviviparity with high reproductive rates (Moreno-Valcarcel et al. 2012). Since the 1960s, mosquitofish has spread around the world and is now widely distributed in various freshwater habitats (Pyke 2005). Many countries and organizations have listed it as an invasive species with considerable influence on local ecosystems.

The subjects used in this study were the offspring of a wild population of mosquitofish collected from an aquaculture pond of approximately 300 m^2 near Gongtan, Shanghai (120.99°E, 31.01°N) in May 2019 (Figure 1). A total of 150 gravid females were net-captured and brought to the laboratory at Anhui University (117.18°E, 31.77°N), where groups of 10 females were housed in individual tanks (37 × 27 × 13.5 cm) filled with oxygenated tap water at approximately 23–25°C. We fed the fish fine-grained commercial food (TIDDLER, Weifang YEE Pet Products Co., Ltd., China; 42% crude protein, 5% crude fat, 5% crude fibers, 11% ash) every morning and exposed them to a natural photoperiod (~14:10 L:D).

We frequently checked the housing tanks of mother fish and collected a total of 480 newborns within 1 week. These newborns were immediately transferred to 24 net tanks (blocks: 26 × 15 × 15 cm, mesh size: 0.5 mm; 20 fish in each block) evenly placed in 2 200-L plastic tanks (rearing tank, 90 × 74 × 30 cm) filled with a depth of 13-cm oxygenated tap water. To avoid the potential influence of genetic factors, we equally allocated the offspring of each mother into the 2 rearing tanks and placed the fries into different blocks so that no fish in the same block were given birth by the same mother. Due to the stocking procedure, the sex ratios among the blocks were considered to be equal. The newborns were fed brine shrimp nauplii and fine-grained commercial food (Weifang YEE Pet Products Co.,

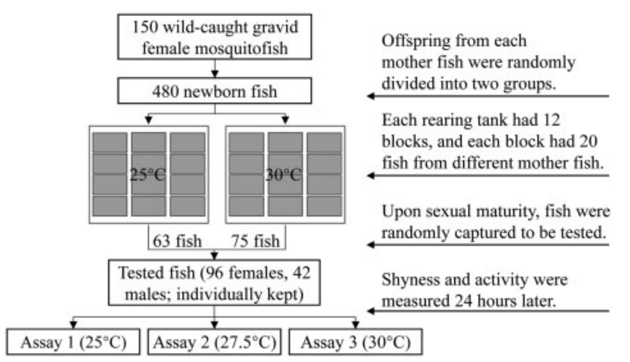

Figure 1. Overview diagram of the experiments.

Ltd.) and were exposed to a 14:10 h light:dark photoperiod. One black, opaque, cylindrical refuge chamber (height: 5 cm; diameter: 7 cm) was placed in each block as a refuge for the fish, and a layer of ceramsite (density: 1.8–2.0 g/cm^3; diameter: 1 mm) was placed at the bottom of each net tank to improve water quality. Because the mean water temperature in the freshwater lakes in our study area in June is approximately 25°C, we maintained the water temperature in one rearing tank at 25°C and another one at 30°C throughout the rearing period. Each rearing tank had its own water recycling and temperature regulation system. In each rearing tank, the oxygen saturation was maintained at 6.77 ± 0.36 mg/L, the pH at 7.36 ± 0.12, and ammonia nitrogen below 0.1 mg/L.

In July when the reared newborns reached sexual maturity, we randomly net-caught subjects from each block to be used in the following behavioral experiments. Before and between experiments, the selected fish were individually kept in labeled black opaque tanks (height: 9 cm; diameter: 15 cm; hereafter holding container) with transparent lids filled with oxygenated tap water. A black, opaque, cylindrical refuge chamber (height: 5 cm; diameter: 7 cm) was also placed in the center of the holding container. The fish were given at least 24 h to acclimate to the holding container. They were exposed to a 14:10 h light:dark photoperiod and were not fed 12 h before the experiments.

Assays for shyness and exploration

We measured shyness and exploration in an opaque white plastic tank (37 cm long × 30 cm wide × 20 cm high) filled with 3 cm of oxygenated tap water which was exchanged between trials to avoid any effect of chemical signals released by previous subjects on subsequent ones. One black, opaque, cylindrical refuge chamber (height: 5 cm; diameter: 7 cm; hereafter, starting refuge) was fixed to one end of the experiment tank and the rest of the tank was furnished with novel structures to enrich the environment. To avoid the potential effects of habituation toward the same environment, we used different novel structures, that is, gravel, plastic sheets, and fresh lotus leaves in different trials for the same fish. These materials were scattered in the same configuration for different subjects. During each trial, the experimenter was shielded by an opaque curtain to avoid any interference on the tested fish. There was a sliding trapdoor (3 × 3 cm) on the starting refuge connected to a piece of fishing line that enabled the experimenter to remotely open the refuge to allow fish to swim out of the chamber and toward the arena. A camera (Sony HDR-CX510, 55× extended zoom, Sony Corporation, Tokyo, Japan) was suspended above the center of the experimental tank to record the behavior of the fish during the experiments.

At the beginning of a trial, a randomly selected fish was gently introduced to the closed starting refuge, and then the camera was switched on. The subject was allowed to acclimate for 5 min, after which the observer remotely opened the trapdoor of the starting refuge and left it open until the end of the trial. The time taken by the subject to emerge out of the starting refuge (latency) was used to measure its shyness, the opposite of boldness. Latency is commonly used to measure shyness, with bolder subjects emerging sooner from the shelter (Brown and Braithwaite 2004a; Brown et al. 2007). We considered that a fish had emerged from the starting refuge when its entire body had crossed the trapdoor. All the tested fish swam out of the refuge within 10 min. The camera continued to record the movement of the subject for another 10 min (i.e., exploration assay) after it had left the refuge. After the exploration assay, the subject was immediately transferred back to its holding container. We extracted 600 image stacks from the 10-min movement videos (1 frame per second), and used Image J (http://rsbweb.nih.gov/ij/) to mark the location of the fish head in each frame to delineate its movement pathway. Similar to Edenbrow and Croft (2013) and consistent with Xu et al. (2020), we used the total pathway length to quantify the exploration score of the focal subject. We acknowledge that the measurement of exploration may concurrently include some extents of activity because animals should be active while exploring (Carter et al. 2013). However, we referred to this test as exploration behavior because it was tested in an unfamiliar, novel, environment in which the distance covered has been proposed to be a measure of exploration (Sih et al. 2004; Réale et al. 2007).

The above assays were conducted in a laboratory with sufficient light and no interference. Each subject was assayed 3 times, each in 1 successive day, and the water temperatures were 25°C, 27.5°C, and 30°C, respectively. To reduce the effect of changes in water temperature on fish behaviors, the fish reared at 25°C were tested in water temperatures with an ascending order, while those reared at 30°C with a descending order. The assay sequence for each fish was random on the first trial day and fixed on following days. The fish were fed commercial food after each trial. On day 3, the body length (accurate to 0.1 mm) of each subject was measured after the 3 trials.

Ethical statement

Mosquitofish is an invasive species that is prohibited from being released into natural water bodies in China. Thus, no review was required from the ethics committee (Ministry of Environmental Protection of the People's Republic of China 2016, Index No. 000014672/2016-01463). The behavioral experiments were conducted with the approval of the Institutional Animal Care and Use Committee of Anhui University (IACUC, AHU), and no fish were harmed during the experiments.

Statistical analyses

Repeatability is commonly used as a measure of within-individual behavioral consistency, where individual identity is a grouping factor (Stoffel et al. 2017). Here, we employed the function *rpt* in the R package *rptR* (Stoffel et al. 2017) to measure the repeatability of shyness and exploration, with body length as the fixed factor and block ID and individual ID as random effects. The *nboot* argument was set to be 1,000 bootstraps to control the number of parametric bootstrap iterations for the confidence interval estimations. We used the function *corr.test* in the package *psych* (Revelle 2019) to measure the Spearman rank correlation between the 2 behaviors.

For the body lengths and the 2 behavioral traits, we used the Shapiro–Wilk test to examine the assumption of normality. As the data did not fit normal distributions, we performed Mann–Whitney *U* tests to compare the body lengths between sexes and between rearing temperatures (Mollan et al. 2020). We fitted a generalized linear mixed model (GLMM) with a Gaussian error structure to test how each behavior was influenced by rearing temperature, sex, and body length, which were identified as fixed effects in the model. The block ID and individual ID of the fish were included in the models as random effects (Niemelae et al. 2019). We fitted the models and tested the significance of the effects using the function *glmmPQL* in the package *MASS* (Venables and Ripley 2002). All statistical analyses were performed in R 3.6.1 (R Development Core Team 2019), and the significance level was set to $P < 0.05$.

Results

Sampling information

We quantified behavioral traits for a total of 138 mature mosquitofish collected from the rearing tanks. Specifically, we randomly selected 4 females from each block, totaling 96 individuals. Due to the highly female-skewed sex ratio in each rearing tank, the number of males in each tank was less than 4, and all of them (i.e., 42 individuals) were used in the experiments. Among these subjects, 75 were reared at high temperatures, while 63 were reared at low temperatures (Table 1). Body length differed between females and males ($W = 21,\ 258$; $P < 0.005$), but not between high- and low-temperature treatments ($W = 20,\ 025$; $P = 0.299$).

Behavioral consistency and correlation

Across the behavioral assays, female mosquitofish reared at low temperatures exhibited significant repeatability in shyness and exploration, whereas females at high temperatures did not. Male fish only showed marginally significant repeatability in shyness when they were reared at low temperatures (Table 2). Shyness was negatively correlated with exploration in females reared at both high and low temperatures, while the negative correlation for males was only found when they grew up at low temperatures (Figure 2).

Effects of factors on behavioral traits

Overall, the fixed factors, that is, body length, rearing temperature, and sex, failed to explain the variance in shyness (Table 3). The fish reared at high temperatures showed higher levels of exploration, which did not differ between sexes and was not affected by body length (Table 3 and Figure 3).

Discussion

Our study provides further evidence for the existence of personality in mosquitofish, and reveals that environmental temperature during early life can significantly shape personality traits of this species in their adulthood (Table 2 and Figure 3). Animal personality refers to repeatable behavioral differences among individuals and has widely been found in the animal kingdom (Sih et al. 2004; Sauerberger and Funder 2017). Empirical studies have found that the inter-individual behavioral differences generally contribute to more than one-third of the phenotypic behavioral variance within populations (Bell et al. 2009). Repeatability varies among behavioral traits and can be affected by many factors such as age, sex, and the interval between observations (Bell et al. 2009). We found that the fish reared in low temperatures exhibited more significant behavioral differences among individuals, while higher temperatures of the growth environment could trigger behavioral stability to vary (Table 2). This finding suggests that temperature should be a key factor that influences the personality of ectothermic species (Dosmann et al. 2015). Previous studies have also found that animals behave more variably at higher temperatures (Katz et al. 2017). The increased level of behavioral plasticity under higher temperatures might strengthen the ability of animals to better cope with the changing environment. Taken in this sense, global warming might be beneficial for invasive species to colonize more habitats.

Apart from repeatability in behavioral traits, we found a significant negative correlation between shyness and exploration for male fish at low temperatures and for females at both temperatures (Figure 2). The negative correlation provides further evidence for behavioral syndromes in mosquitofish (Cote et al. 2013; Xu et al. 2020). Behaviors often do not evolve independently, and behavioral syndromes appear to be widespread in nature (Sih et al. 2004; Sinervo 2010). For example, larger individuals of zebrafish *Danio rerio* are bolder in the face of risks and are more active and aggressive when confronted with enemies (Polverino et al. 2016). The study of correlations between behaviors may promote a comprehensive understanding of how animals adapt to their environments (Brommer et al. 2014). Our findings indicate that bolder fishes were more explorative than timid ones, which may be controlled by the same endocrine state (e.g., hormones). Shyness means unwillingness to take risks, and therefore shyer individuals tend to explore less in novel environments which may be dangerous (Dammhahn and Almeling 2012).

As expected, we found a significant effect of rearing temperature on the average tendency of exploration, that is, the fish growing at high temperatures explored more than those growing at low temperatures. This finding indicates that mosquitofish can modify their explorative behaviors, to a certain extent, to adapt to varying external environments. The underlying mechanism may be related to the metabolic rate of the animals (Houston 2010). When the temperature rises, the metabolic cost of animals increases, and more energy will be consumed, which requires animals to obtain more food resources. These circumstances induce higher levels of exploration, which are beneficial for animals to obtain food (Biro et al. 2010). In the context of global warming, increasing exploration may affect the migration pattern and distribution of the species, and even

Table 2. Repeatability of behavioral traits in mosquitofish reared at different temperatures

Sex	Repeatability	Shyness		Exploration	
		25°C	30°C	25°C	30°C
Female	*R*	0.24	0.05	0.29	0.01
	Standard error	0.09	0.07	0.10	0.05
	95% confidence interval	0.04, 0.41	0, 0.22	0.06, 0.44	0, 0.18
	P-value	**0.003**	0.294	***P* < 0.001**	0.451
Male	*R*	0.18	0	0.05	0
	Standard error	0.12	0.09	0.09	0
	95% confidence interval	0, 0.41	0, 0.29	0, 0.28	0, 0
	P-value	0.068	1.000	0.314	1.000

Significantly repeatable behaviors are displayed in bold.

Table 1. Sampling information and mean behavioral traits (± standard deviation, *SD*) in mosquitofish reared at different temperatures

Sex	Rearing temperatures	Sample size	Body length (mm)	Shyness (s)	Exploration (cm)
Female	25°C	48	16.8 (±2.1)	82.6 (±68.9)	1103.7 (±380.3)
	30°C	48	16.8 (±1.8)	83.5 (±88.1)	1244.1 (±400.7)
Male	25°C	27	15.9 (±1.6)	103.3 (±73.6)	1061.8 (±369.8)
	30°C	15	16.2 (±1.3)	86.6 (±86.3)	1224.2 (±469.9)

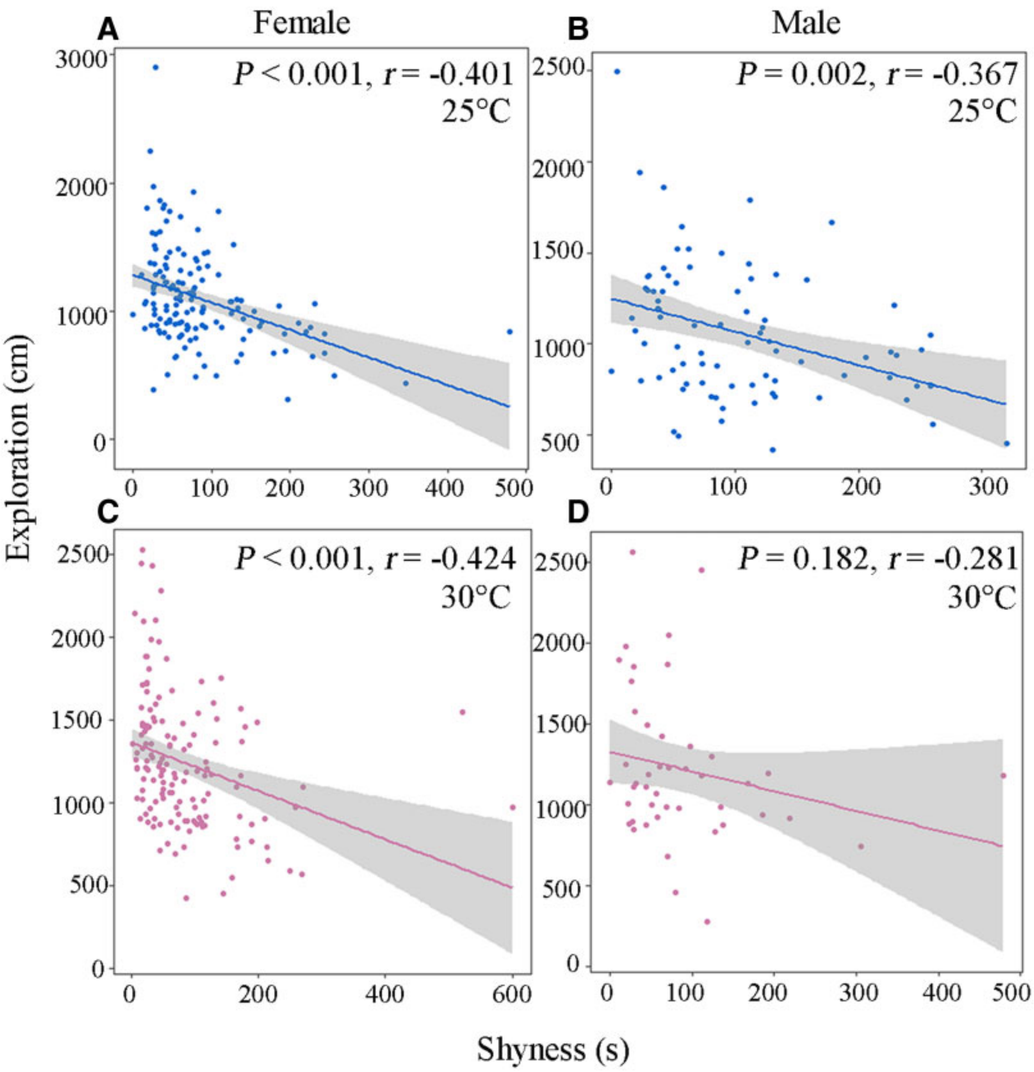

Figure 2. Correlations between shyness and exploration in mosquitofish reared at different temperatures.

Table 3. The effects of rearing temperature, sex, and body length on shyness and exploration in mosquitofish

	Explanatory variables	Coefficient	*SE*	*df*	*t*-value	*P*-value
Shyness	Rearing temperature (higher temperature)	−4.73	8.66	16	−0.55	0.590
	Sex (male)	14.76	9.53	118	1.54	0.120
	Body length	0.10	2.36	118	0.42	0.673
Exploration	Rearing temperature (higher temperature)	173.10	61.60	16	2.81	**0.013**
	Sex (male)	−32.48	48.88	118	−0.66	0.508
	Body length	8.53	12.46	118	0.68	0.495

accelerate its invasion rate. Contrary to our expectations, however, shyness of mosquitofish did not differ between rearing temperatures. This might be explained by that the fish growing at both temperatures had experienced no predation risks during the whole rearing periods. They might realize no risks when they decided to enter the novel arena during the experiments, and thus they behaved similarly.

We found no effects of body length or sex on shyness and exploration of mosquitofish. Some studies have suggested that body size and sex might influence the 2 behavioral traits (Lopez et al. 2005; Polverino et al. 2016). The correlation between behaviors and body size is often explained by the metabolic hypothesis that smaller individuals are expected to emerge sooner from shelters and explore more because of their faster metabolic rates and less energy reserve (Krause et al. 1998; Skalski and Gilliam 2002; Brown and Braithwaite 2004b). Some studies have found that, however, larger individuals are bolder and more explorative because of stronger competition abilities (Colleter and Brown 2011). Inconsistency among studies also exists for the effect of sex. Some studies have found that females tend to be shyer and less explorative (Diaz Pauli et al. 2019; Xu et al. 2020), while others have found the opposite pattern (Dall 2004). Generally, effects of environmental factors on behaviors may interact with each other, vary among species, and change with ontogeny (Pearish et al. 2013; Castillo-Guerrero et al. 2016). Our finding is consistent with some studies (Ingley et al. 2014; Hamada and Kuriwada 2019), and may imply that, thus far, generalizations can hardly be made about the effects of body size and sex on shyness and exploration, and that the underlying mechanisms deserve further studies.

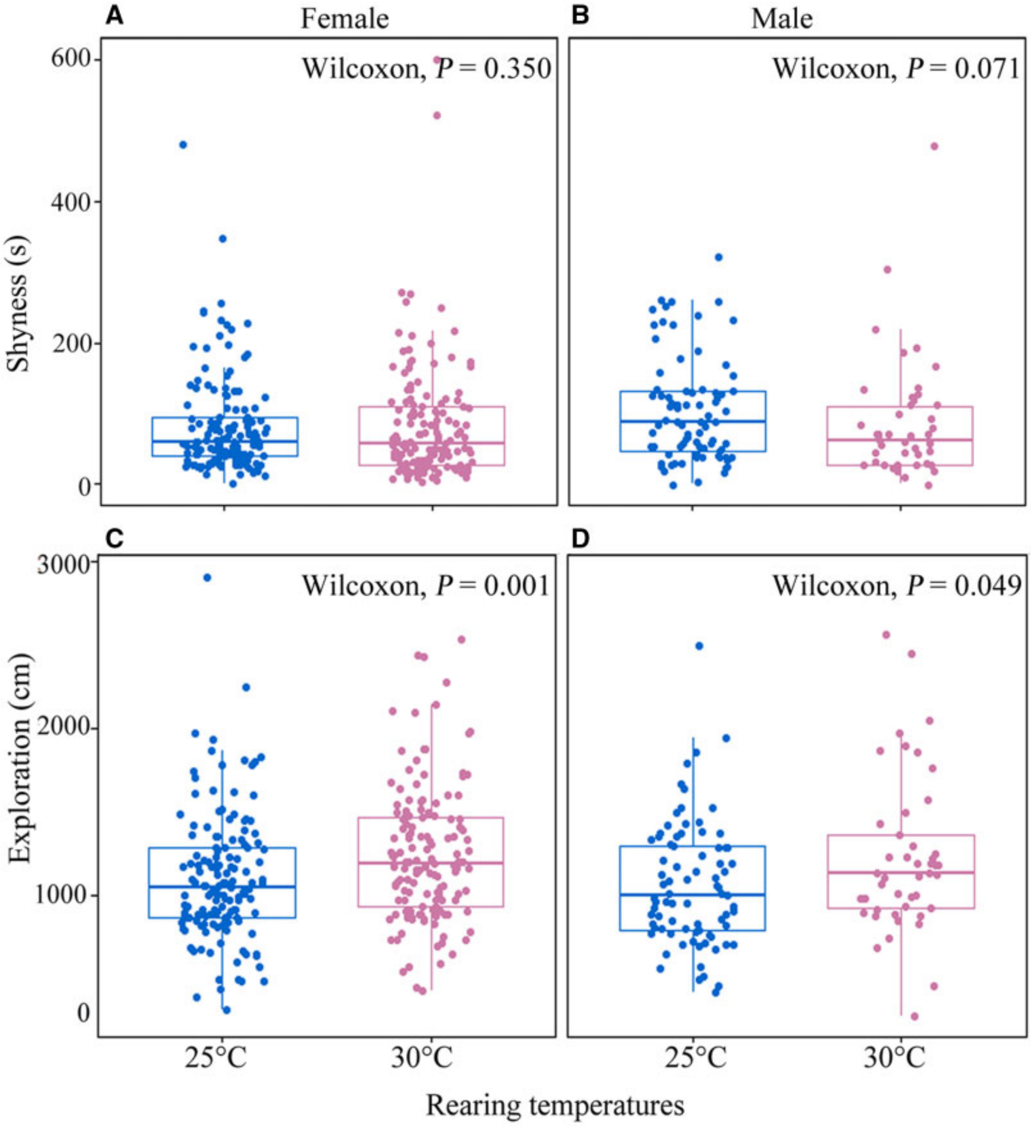

Figure 3. Scores of behavioral traits in mosquitofish reared at different temperatures.

In conclusion, our study provides further evidence for the existence of personality as well as behavioral syndromes in mosquitofish. The behaviors of the fish reared at low temperatures were more repeatable than those at high temperatures, suggesting that environmental temperature in early life stages should be a key factor that influences animal personality. Except for males reared at high temperatures, shyness was negatively correlated with exploration, indicating that the 2 behaviors comprise a behavioral syndrome in this species. Fish reared in different temperatures did not differ in shyness, but the individuals reared at high temperatures were more explorative. We detected no effects of body length or sex on the 2 behavioral traits. Our results suggest that environmental temperature in the early-life period could shape the development of animal personality and modify the average tendency of the behavioral traits.

Author Contributions

C.L. and H.L. conceived and designed the experiments. Y.W., H.L., and X.Z. performed the experiments and carried out the data analyses. H.L., C.L., and F.Z. wrote the manuscript. All authors have contributed substantially to the work and approved the final submission.

Acknowledgments

The authors thank Binbin Zhao for his help during the fish rearing, and Daode Zha and Zhiwen Yuan for their helpful comments and suggestions.

Funding

This work was supported by the National Natural Science Foundation of China (grant numbers 31970500, 31770571, and 31301897), the Open Fund for Discipline Construction from the Institute of Physical Science and Information Technology, Anhui University, and Biodiversity Investigation, Observation and Assessment Program of Ministry of Ecology and Environment of China.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

Conflict of interest statement

We declare no potential conflicts of interest.

References

Amat I, Desouhant E, Gomes E, Moreau J, Monceau K, 2018. Insect personality: what can we learn from metamorphosis? *Curr Opin Insect* **27**: 46–51.

Bell AM, Dingemanse NJ, Hankison SJ, Langenhof MBW, Rollins K, 2011. Early exposure to nonlethal predation risk by size-selective predators increases somatic growth and decreases size at adulthood in threespined sticklebacks. *J Evol Biol* **24**: 943–953.

Bell AM, Hankison SJ, Laskowski KL, 2009. The repeatability of behaviour: a meta-analysis. *Anim Behav* **77**: 771–783.

Bell AM, Sih A, 2007. Exposure to predation generates personality in threespined sticklebacks *Gasterosteus aculeatus*. *Ecol Lett* **10**: 828–834.

Bierbach D, Laskowski KL, Wolf M, 2017. Behavioural individuality in clonal fish arises despite near-identical rearing conditions. *Nat Commun* **8**: 69–74.

Biro PA, Beckmann C, Stamps JA, 2010. Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proc R Soc B Biol Sci* **277**: 71–77.

Briffa M, Bridger D, Biro PA, 2013. How does temperature affect behaviour? Multilevel analysis of plasticity, personality and predictability in hermit crabs. *Anim Behav* **86**: 47–54.

Briffa M, Weiss A, 2010. Animal personality. *Curr Biol* **20**: R912–R914.

Brommer JE, Karell P, Ahola K, Karstinen T, 2014. Residual correlations, and not individual properties, determine a nest defense boldness syndrome. *Behav Ecol* **25**: 802–812.

Brown C, Braithwaite VA, 2004. Size matters: a test of boldness in eight populations of the poeciliid *Brachyraphis episcopi*. *Anim Behav* **68**: 1325–1329.

Brown C, Burgess F, Braithwaite VA, 2007. Heritable and experiential effects on boldness in a tropical poeciliid. *Behav Ecol Sociobiol* **62**: 237–243.

Carere C, Drent PJ, Koolhaas JM, Groothuis TGG, 2005. Epigenetic effects on personality traits: early food provisioning and sibling competition. *Behaviour* **142**: 1329–1355.

Carter AJ, Feeney WE, Marshall HH, Cowlishaw G, Heinsohn R, 2013. Animal personality: what are behavioural ecologists measuring? *Biol Rev* **88**: 465–475.

Castillo-Guerrero JA, Lerma M, Mellink E, Suazo-Guillen E, Penaloza-Padilla EA, 2016. Environmentally-mediated flexible foraging strategies in brown boobies in the Gulf of California. *Ardea* **104**: 33–47.

Cavallo C, Dempster T, Kearney MR, Kelly E, Booth D et al., 2015. Predicting climate warming effects on green turtle hatchling viability and dispersal performance. *Funct Ecol* **29**: 768–778.

Colleter M, Brown C, 2011. Personality traits predict hierarchy rank in male rainbowfish social groups. *Anim Behav* **81**: 1231–1237.

Cote J, Fogarty S, Tymen B, Sih A, Brodin T, 2013. Personality-dependent dispersal cancelled under predation risk. *Proc R Soc B Biol Sci* **280**: 20132349.

Dall SRX, 2004. Behavioural biology: fortune favours bold and shy personalities. *Curr Biol* **14**: R470–R472.

Dammhahn M, Almeling L, 2012. Is risk taking during foraging a personality trait? A field test for cross-context consistency in boldness. *Anim Behav* **84**: 1131–1139.

Diaz Pauli B, Garric S, Evangelista C, Vollestad LA, Edeline E, 2019. Selection for small body size favours contrasting sex-specific life histories, boldness and feeding in medaka *Oryzias latipes*. *BMC Evol Biol* **19**: 127.

Dingemanse NJ, Kazem AJN, Réale D, Wright J, 2010. Behavioural reaction norms: animal personality meets individual plasticity. *Trends Ecol Evol* **25**: 81–89.

Dingemanse NJ, Réale D, 2005. Natural selection and animal personality. *Behaviour* **142**: 1159–1184.

Dosmann AJ, Brooks KC, Mateo JM, 2015. Within-individual correlations reveal link between a behavioral syndrome, condition, and cortisol in free-ranging Belding's ground squirrels. *Ethology* **121**: 125–134.

Edenbrow M, Croft DP, 2013. Environmental and genetic effects shape the development of personality traits in the mangrove killifish *Kryptolebias marmoratus*. *Oikos* **122**: 667–681.

Fawcett TW, Frankenhuis WE, 2015. Adaptive explanations for sensitive windows in development. *Front Zool* **12**: S3.

Garcia-Berthou E, Alcaraz C, Pou-Rovira Q, Zamora L, Coenders G et al., 2005. Introduction pathways and establishment rates of invasive aquatic species in Europe. *Can J Fish Aquat Sci* **62**: 453–463.

Garduno-Paz MV, Couderc S, Adams CE, 2010. Habitat complexity modulates phenotype expression through developmental plasticity in the threespine stickleback. *Biol J Linn Soc* **100**: 407–413.

Gracceva G, Koolhaas JM, Groothuis TGG, 2011. Does the early social environment affect structure and consistency of personality in wild-type male rats? *Dev Psychobiol* **53**: 614–623.

Hamada T, Kuriwada T, 2019. Boldness to predator is not significantly correlated with mating behaviour in a simultaneously hermaphroditic snail. *Ethol Ecol Evol* **31**: 469–478.

Hoffmann AA, Sgro CM, 2011. Climate change and evolutionary adaptation. *Nature* **470**: 479–485.

Houston AI, 2010. Evolutionary models of metabolism, behaviour and personality. *Phil Trans R Soc B* **365**: 3969–3975.

Ingley SJ, Rehm J, Johnson JB, 2014. Size doesn't matter, sex does: a test for boldness in sister species of *Brachyrhaphis* fishes. *Ecol Evol* **4**: 4361–4369.

Jolles JW, Boogert NJ, Sridhar VH, Couzin ID, Manica A, 2017. Consistent individual differences drive collective behavior and group functioning of schooling fish. *Curr Biol* **27**: 2862–2868.

Katz N, Pruitt JN, Scharf I, 2017. The complex effect of illumination, temperature, and thermal acclimation on habitat choice and foraging behavior of a pit-building wormlion. *Behav Ecol Sociobiol* **71**: 137.

Killen SS, Atkinson D, Glazier DS, 2010. The intraspecific scaling of metabolic rate with body mass in fishes depends on lifestyle and temperature. *Ecol Lett* **13**: 184–193.

King AJ, Furtbauer I, Mamuneas D, James C, Manica A, 2013. Sex-differences and temporal consistency in stickleback fish boldness. *PLoS ONE* **8**: e8116.

Krause J, Loader SP, McDermott J, Ruxton GD, 1998. Refuge use by fish as a function of body length-related metabolic expenditure and predation risks. *Proc R Soc B Biol Sci* **265**: 2373–2379.

Kvingedal E, Einum S, 2011. Prior residency advantage for Atlantic salmon in the wild: effects of habitat quality. *Behav Ecol Sociobiol* **65**: 1295–1303.

Langenhof MR, Apperloo R, Komdeur J, 2016. Small variations in early-life environment can affect coping behaviour in response to foraging challenge in the three-spined stickleback. *PLoS ONE* **11**: e0147000.

Lopez P, Hawlena D, Polo V, Amo L, Martin J, 2005. Sources of individual shy-bold variations in antipredator behaviour of male Iberian rock lizards. *Anim Behav* **69**: 1–9.

Mollan KR, Trumble IM, Reifeis SA, Ferrer O, Bay CP et al., 2020. Precise and accurate power of the rank-sum test for a continuous outcome. *J Biopharm Stat* **30**: 639–648.

Moreno-Valcarcel R, Oliva-Paterna FJ, Arribas C, Fernandez-Delgado C, 2012. Length–weight relationships for 13 fish species collected in the Donana marshlands (Guadalquivir estuary, SW Spain). *J Appl Ichthyol* **28**: 663–664.

Niemelae PT, Niehoff PP, Gasparini C, Dingemanse NJ, Tuni C, 2019. Crickets become behaviourally more stable when raised under higher temperatures. *Behav Ecol Sociobiol* **73**: 81.

Pearish S, Hostert L, Bell AM, 2013. Behavioral type–environment correlations in the field: a study of three-spined stickleback. *Behav Ecol Sociobiol* **67**: 765–774.

Polverino G, Bierbach D, Killen SS, Uusi-Heikkila S, Arlinghaus R, 2016. Body length rather than routine metabolic rate and body condition correlates with activity and risk-taking in juvenile zebrafish *Danio rerio*. *J Fish Biol* **89**: 2251–2267.

Pyke GH, 2005. A review of the biology of *Gambusia affinis* and *G-holbrooki*. *Rev Fish Biol Fish* **15**: 339–365.

Pyke GH, 2008. Plague minnow or mosquito fish? A review of the biology and impacts of introduced *Gambusia* species. *Annu Rev Ecol Evol Syst* **39**: 171–191.

R Development Core Team, 2019. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Available from www.r-project.org.

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ, 2007. Integrating animal temperament within ecology and evolution. *Biol Rev* **82**: 291–318.

Revelle W, 2019. *Psych: Procedures for Psychological, Psychometric, and Personality Research*. R package version 1.9.12. Evanston, Illinois: Northwestern University.

Sauerberger KS, Funder DC, 2017. Behavioral change and consistency across contexts. *J Res Pers* **69**: 264–272.

Sih A, Bell AM, Johnson JC, Ziemba RE, 2004. Behavioral syndromes: an integrative overview. *Q Rev Biol* **79**: 241–277.

Sinervo B, 2010. Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328**: 1354–1354.

Skalski GT, Gilliam JF, 2002. Feeding under predation hazard: testing models of adaptive behavior with stream fish. *Am Nat* **160**: 158–172.

Smith BR, Blumstein DT, 2008. Fitness consequences of personality: a meta-analysis. *Behav Ecol* **19**: 448–455.

Stoffel MA, Nakagawa S, Schielzeth H, 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods Ecol Evol* **8**: 1639–1644.

Venables WN, Ripley BD, 2002. *Modern Applied Statistics with S*. 4th edn. New York: Springer-Verlag.

Wolf M, Weissing FJ, 2012. Animal personalities: consequences for ecology and evolution. *Methods Ecol Evol* **27**: 452–461.

Xu WJ, Yao Q, Zhang WW, Zhang F, Li HF et al., 2020. Environmental complexity during early life shapes average behavior in adulthood. *Behav Ecol* published online (doi: 10.1093/beheco/araa108).