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Predation experience underlies the relationship between locomotion capability and survival

Cheng Fu, Zhen-Dong Cao, Shi-Jian Fu*

Laboratory of Evolutionary Physiology and Behavior, Chongqing Normal University, Chongqing, China

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ABSTRACT

The positive relationship between locomotion performance and survival under predation has long been suggested yet seldom demonstrated with direct evidence. We investigate the effects of predator exposure on locomotion capacity (both fast-start escape and critical swimming performance), survival under predation and the relationships between these factors in juvenile Chinese bream (*Parabramis pekinensis*). This study aims to test whether there is a positive relationship between the above factors and whether such relationships are context dependent (i.e., with or without 20 d of predator exposure). We found that predator-exposed Chinese bream showed higher rates of survival under predation and improved fast-start swimming performance compared with individuals not exposed to predation. At individual level, no relationship was found between survival and any locomotion performance component in the no-predator group, but mean fast-start swimming speed, maneuverability and responsiveness were all positively related to survival in the predator group after 20 d of exposure. This finding indicates that the recognition of and vigilance for predators achieved through predation experience can be crucial preconditions for prey to employ the fast-start escape response, especially to escape ambush predators. Furthermore, a tradeoff was observed between the critical and fast-start swimming performances in the predator group, but not in the no-predator group, which may have been due to the intensified competition throughout the entire locomotion-support system (e.g., energy, proportions of slow- and fast-twitch muscle fibers) between critical and fast-start swimming because the increased demand for fast-start escape capacity constrains (or compromises) critical swimming performance under the threat of predation.

1. Introduction

The effects of predators on prey have been observed to lead to phenotypic and (or) genetic changes in a wide array of traits at the whole- and sub-organismal levels (Brown et al., 2007; Langerhans et al., 2007; Oufiero et al., 2011). Locomotor performance, one of the crucial survival-determining traits for animals, is expected to respond to predation (Domenici et al., 2008; Langerhans, 2009a; Fu et al., 2015). For instance, a stronger swimming performance (e.g., fast-start) has been observed in fish in habitats with high predation pressure (Domenici et al., 2008). Induced defenses in locomotion that are plastic responses to short-term predation risk are also important for survival but have received less attention, specifically pertaining to the question of whether improved locomotion connotes higher survival capacity. The first objective of this study was to test whether improved locomotion leading to higher rates of survival could be caused by short-term predator exposure.

The swimming of fish species can be classified as steady or unsteady (Domenici and Kapoor, 2010). In nature, steady swimming is commonly employed when fish remain in place against a current, search for food and migrate (Plaut, 2001; Kieffer, 2010; Dalziel and Schulte, 2012), and the critical swimming speed (U_{crit}) is widely used to evaluate steady swimming in fish (Brett, 1964; Plaut, 2001; Lee et al., 2003; Dalziel and Schulte, 2012; Cai et al., 2014). Swimming performance during the U_{crit} protocol is powered aerobically for most of the trial and is probably limited by slow-twitch muscle fibers, oxygen delivery and/or metabolite and waste-product flux (Komi, 1984; Reidy et al., 2000). Unsteady swimming is commonly employed in social interactions, predator avoidance and when navigating structurally complex environments (Blake, 2004; Domenici and Kapoor, 2010). Fast-start escape performance is one of the most thoroughly investigated measurements of unsteady swimming in fish (Webb, 1986; Law and Blake, 1996; Langerhans, 2009a), and it is widely used to assess the performance of a fish in escaping from a predator (Walker et al., 2005;

* Corresponding author at: Laboratory of Evolutionary Physiology and Behavior, Chongqing Key Laboratory of Animal Biology, Chongqing Normal University, 401331 Chongqing City, China.
E-mail address: shijianfu9@cqnu.edu.cn (S.-J. Fu).

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Domenici et al., 2008; Langerhans, 2009a; Domenici and Kapoor, 2010; Domenici et al., 2014). The fast-start response, which is complete in a matter of seconds, is powered by intracellular stores of adenosine triphosphate (ATP) and creatine phosphate and is probably limited by fast-twitch muscle fibers, neuromuscular morphology and physiology (Komi, 1984; Reidy et al., 2000). The variables related to fast-start performance are divided into non-locomotion and locomotion categories, with responsiveness (e.g., response latency) belonging to the former and the latter including maneuverability (e.g., turning rate) and distance-related performance (e.g., speed, acceleration) (Domenici and Kapoor, 2010). Few studies have attempted to directly test the assumption that faster starts increase the probability of evasion, which we term the faster-start hypothesis (Walker et al., 2005). Such a relationship between fast-start performance and survival may be context dependent because fast-start swimming and survival could be asymmetrically modified by biological or abiotic factors (Domenici, 2010). For example, fast-start performance may be improved through predation experience (Fu, 2015; Liu et al., 2016), while survival rate may be more improved because of the combined effects of improved fast-start, vigilance and anti-predator behavior (Lönnstedt et al., 2012; Lee et al., 2017). Thus, the second goal of this study was to investigate the effect of short-term predator exposure on the relationship between fast-start performance and survival capability under predation.

Aside from fast-start swimming, increased U_{crit} has also been proposed to be crucial in improving fish survival in a recent study (Fu, 2015), but a tradeoff may exist between steady and unsteady swimming performance because of biomechanical, biochemical, or physiological interrelationships between these two swimming types (Clobert et al., 2000; Vanhooydonck et al., 2001; Blake, 2004; Dlugosz et al., 2009). A negative relationship between steady and unsteady swimming capability at the individual level has been demonstrated in some fish species (Reidy et al., 2000; Oufiero et al., 2011). The performance of both critical and fast-start swimming may change under the threat of predation, but whether the relationship between them would also be altered by predation remains poorly understood (Fu et al., 2013b). Therefore, the third objective of this study was to test whether the relationship between critical and fast-start swimming at the individual level would be altered by short-term predator exposure.

The Chinese bream (*Parabramis pekinensis*) is a widely distributed cyprinid in China that has been found in previous studies to exhibit superior kinematic plastic responses to environmental stress (Peng et al., 2014; Wang et al., 2016). The southern catfish (*Silurus meridionalis*) is an ambush carnivore that is widely distributed in southern China and is one of the primary predators of Chinese bream throughout its life history (Ding, 1994). Thus, these two fish species were selected as the prey and predator model in this study. We tested fast-start components, survival capability under predation and the relationships between these factors in juvenile Chinese bream assigned to both no-predator (without predator exposure) and predator (with 20 d of predator exposure) groups to examine our first and second objectives. To fulfill our third objective, we examined the relationships between fast-start and critical swimming components in both no-predator and predator groups. The relationship between critical swimming and survival was also analyzed because of its likely effects on survival.

2. Materials and methods

2.1. Ethical procedures

This study was approved by the Animal Care and Use Committee of the Key Laboratory of Animal Biology of Chongqing (Permit Number: Zhao-20140226-02) and 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.

2.2. Experimental animals and holding

Experimental juvenile Chinese bream (without predation experience) and southern catfish were obtained from local fish farms, kept in the same type of re-circulating water tanks (450 L, length × width × height: 1.5 × 0.6 × 0.5 m) and pre-acclimated for 1 month before the experiments were performed. During this time, the Chinese bream were fed to satiation with dry commercial floating pellets (Tongwei Group, Chengdu, China; composition: 41.2 ± 0.9% protein, 8.5 ± 0.5% lipid, 25.7 ± 1.2% carbohydrate and 12.3 ± 0.4% ash) once daily. The southern catfish were fed to satiation once every 3 d with pieces of freshly killed Chinese bream. The uneaten food and feces were cleared using a siphon 0.5 h after feeding. One-tenth of the water was replaced daily. The water temperature was maintained at 20.0 ± 0.5 °C, and the dissolved oxygen of the water was maintained above 7.0 mg l^{-1}. The light:dark photoperiod was 12 h:12 h.

2.3. Experimental protocol

2.3.1. Predation experience treatment

All tests were performed at a water temperature of 20.0 ± 0.5 °C. Two hundred Chinese bream were marked for identification using PIT (passive integrated transponder) tags (0.03 g, HT-157, Hongteng Corporation, Guangdong, China) three weeks prior to the start of the experiments. No PIT tags were missing, and no fish became infected or died due to tagging during the experiment. One hundred and sixty fish were then randomly selected and divided into no-predator (without predator treatment) and predator (with predator treatment) groups, with 80 fish in each group. The remaining 40 fish were held to replace the Chinese bream consumed by the catfish. All 200 Chinese bream were raised in 10 identical tanks (200 L, length × width × height: 0.8 × 0.5 × 0.5 m) (20 fish per tank, 4 tanks for each group and 2 tanks for supplementary fish). The rearing environments were identical except that a catfish (300–400 g, fish of similar sizes were selected) was placed into the tank of each predator group. During the 20 d when the fish were being raised, all Chinese bream were fed to satiation twice daily at 9:00 and 19:00, and the uneaten food and feces were then collected 30 min later. The catfish in the predator group tank was fed to satiation once every 2 d with pieces of freshly killed Chinese bream at 20:00 to reduce the consumption of the experimental Chinese bream. A camera (C310, Logitech Corporation, Shanghai, China) connected to a computer was fixed on the top of each predator tank to record the number Chinese bream left in each predator group tank, and a corresponding number of fish (selected from the 40 supplementary Chinese bream) of the same size as the consumed individuals were added into the predator group tank as replacements. A total of seven Chinese bream from the predator group were eaten by catfish, four of which were from the supplementary group of individuals over the 20 d of predator exposure treatment. Thus, predator selection imparted negligible effects on the results. After 20 d of treatment, 40 fish (ten from each tank; fish added from the supplemental tanks during the treatment period were excluded) from both the no-predator (6.49 ± 0.13 g, 7.07 ± 0.05 cm) and predator (5.95 ± 0.14 g, 6.96 ± 0.05 cm) groups were randomly selected to measure fast-start and critical swimming performance as well as survival under predation.

2.3.2. Measurement of fast-start swimming performance

After 20 d of treatment and following 48 h of fasting, the individual Chinese bream from both the no-predator and predator groups were transferred into a system designed to measure the fast-start performance of each fish. Individual fish were moved into a rectangular container (approximately 4.6 L, 42 × 31 × 3.5 cm) filled with water, and the water depth was kept at approximately 2 cm to keep the gills of each fish submerged in water while the dorsal side remained outside for the following procedure (Fu et al., 2015). A small, white polystyrene

Table 1
The effects of predation experience on critical (MMR, U_{crit}) and fast-start (V_{max}, A_{max}, V_{mean}, T, turning rate) swimming capacity and survival of juvenile Chinese bream under predation based on ANCOVA.

	N	No predator		Predator	
		Mean ± se	CV (%)	Mean ± se	CV (%)
Critical swimming					
MMR (mgO_2h^{-1})	40	6.89 ± 0.24	21.65	6.22 ± 0.19	19.05
U_{crit} ($cm\,s^{-1}$)	40	65.86 ± 0.77	7.42	65.80 ± 0.87	8.40
Fast-start swimming					
V_{max} ($cm\,s^{-1}$)	40	112.49 ± 4.92[a]	27.68	132.74 ± 5.09[b]	24.24
A_{max} ($m\,s^{-2}$)	40	134.66 ± 8.54	40.1	153.80 ± 10.76	44.26
V_{mean} ($cm\,s^{-1}$)	40	38.64 ± 2.68[a]	43.93	55.62 ± 3.00[b]	34.16
Turning rate ($deg\,s^{-1}$)	40	1067.71 ± 74.21[a]	43.96	1423.43 ± 126.31[b]	56.12
T (s)	40	7.35 ± 1.24	106.98	9.80 ± 1.17	75.63
Survival	40	6.65 ± 0.64[a]	60.78	8.88 ± 0.64[b]	45.44

a, b: Different superscripted letters indicate a significant difference between the no-predator and predator groups.

foam ball (diameter of 1 mm, mass < 0.001 g) was attached with glue to the dorsal side of the fish at the center of mass (CM) (Fu et al., 2015). This procedure lasted for < 1 min, and the fish were then individually transferred to an experimental glass tank (40 × 40 × 15 cm, Supplementary materials, Fig. S1) for 1 h of acclimation prior to being startled (Domenici et al., 2008). Square reference grids (1 × 1 cm) were attached to the floor of the tank, and the sides of the experimental tank were covered with white paper. The depth of the water in the tank was 10 cm. After 1 h of habituation, an escape response was elicited with an electrical impulse (0.55 V cm^{-1}; 50 ms, as determined in a previous study by He et al., 2011) that was manually triggered when the fish was in a holding position in the center of the filming zone. Meanwhile, a high-speed camera (A504K, Basler, Germany; 500 frames s^{-1}) was used to record the entire duration of the response (time span, 2 s). The electrical stimulus was initiated as soon as the light-emitting diode (LED; synchronized with the electrical stimulus) was illuminated (0-ms delay). The resulting sequence of images was then digitized with TpsUtil and TpsDig software (http://life.bio.sunysb.edu/morph) to define the track of the CM in the locomotion performed by the fish during its escape response. The following components were calculated: maximum linear velocity (V_{max}, cm s^{-1}), maximum linear acceleration (A_{max}, m s^{-2}), mean velocity (V_{mean}, cm s^{-1}), turning rate (deg s^{-1}), and response latency (T, ms). The V_{max} and A_{max} components are the maximum velocity and acceleration with which the CM moved during the escape response, respectively. V_{mean} is defined as the mean velocity at which the CM moved during the first 120 ms after the stimulus. V_{max}, A_{max} and V_{mean} were computed using a five-point smoothing regression to smooth the CM displacement data (Lanczos, 1956). The turning rate was defined as the ratio of the stage I angle (the angle between the lines joining the CM and the snout at the beginning of the response and at the end of the turn during the first body bend) and the stage I duration (Domenici et al., 2008). Component T was defined as the time elapsed between the initiation of the stimulus (LED light) and the time when escape behavior was observed (Fu et al., 2013b). A shorter T indicates a stronger fast-start performance.

2.3.3. Measurement of critical swimming performance

After the measurement of the fast-start performance, the fish were transferred to a Blazka-type swim tunnel respirometer to measure critical swimming performance after 48 h of recovery. The U_{crit} and maximum metabolic rate (MMR) were calculated. The swim respirometer was previously described (Fu et al., 2011; Fu et al., 2013a), and it was constructed from clear plastic poly-methyl-methacrylate. A circulating water flow was generated in the tunnel (a total volume of 3 L) by an acrylic propeller attached to a variable speed pump, which was connected to a stepper motor driver controlled by a computer. A program was used to regulate the speed of the pump by emitting a specified electric pulse, thus determining the water velocity. A high-speed digital camera (EX-ZR200, Casio, Japan) in video mode was employed to calibrate the water velocity from the pump controller by tracking small, black agar balls (with the same density as water) in the current. Then, the relationship between the water velocity and the number of electric pulses could be represented as a linear equation. Thus, the water velocity could be determined by setting a specific electric pulse output. A honeycomb screen was secured at both ends of the swimming chamber to reduce turbulence and to ensure uniform water velocity across the chamber. Each individual fish was placed downstream of the propeller in a swimming chamber with a 19.9-cm^2 cross-sectional area, in which the water temperature was controlled to within ± 0.5 °C using a water bath connected to a stainless-steel heat exchanger. The fish were individually transferred to the swim tunnel and allowed to recover and acclimate for 4 h. During this time, aerated water continually flowed through the respirometer at a water speed of 7 cm s^{-1} (approximate 1 body length).

After 4 h of acclimation, the water velocity was increased in 7-cm s^{-1} increments every 20 min until the fish became fatigued. Fatigue was defined as the time at which the fish failed to move from the rear honeycomb screen of the swimming chamber for 20 s (Lee et al., 2003). U_{crit} was calculated for individual fish using Brett's equation (Brett, 1964):

$$U_{crit} = V + (t/T)\ \Delta V \tag{1}$$

where V is the highest speed at which the fish swam for the full time period (cm s^{-1}); ΔV is the velocity increment (7 cm s^{-1}); T is the prescribed period of swimming at each speed (20 min); and t is the time for which the fish swam at the final speed (min).

The swim tunnel was designed to switch between a closed mode and an open mode, with the former being used for respirometry and the latter to replenish oxygen levels. In the closed mode, a small volume of water was drawn from the sealed respirometer with a pump, forced past a dissolved oxygen probe (HQ30; Hach, CO, USA) housed in a sealed temperature-controlled chamber and then returned to the respirometer. The oxygen concentration (mg L^{-1}) was recorded once every 2 min. The metabolic rate ($\dot{M}_{O2}$, mg h^{-1}) of individual fish while swimming was calculated from the oxygen depletion according to the equation:

$$\dot{M}_{O2} = 60\,(S_t - S_0)v \tag{2}$$

where S_t (slope, mg L^{-1} min^{-1}) and S_0 represent the decrease in the dissolved oxygen content of the water per min with and without fish, respectively. These values were obtained from the linear regressions between time (min) and the dissolved oxygen content (mg L^{-1}). The S_0 is primarily caused by bacteria. Before the fish was transferred into the respirometer and after the fish was transferred out when exhausted, the slope of the empty respirometer was calculated twice. Then, the S_0 of each speed could be calculated according to the growth rate of the slope. The S_0 of each fish under each water velocity was calculated

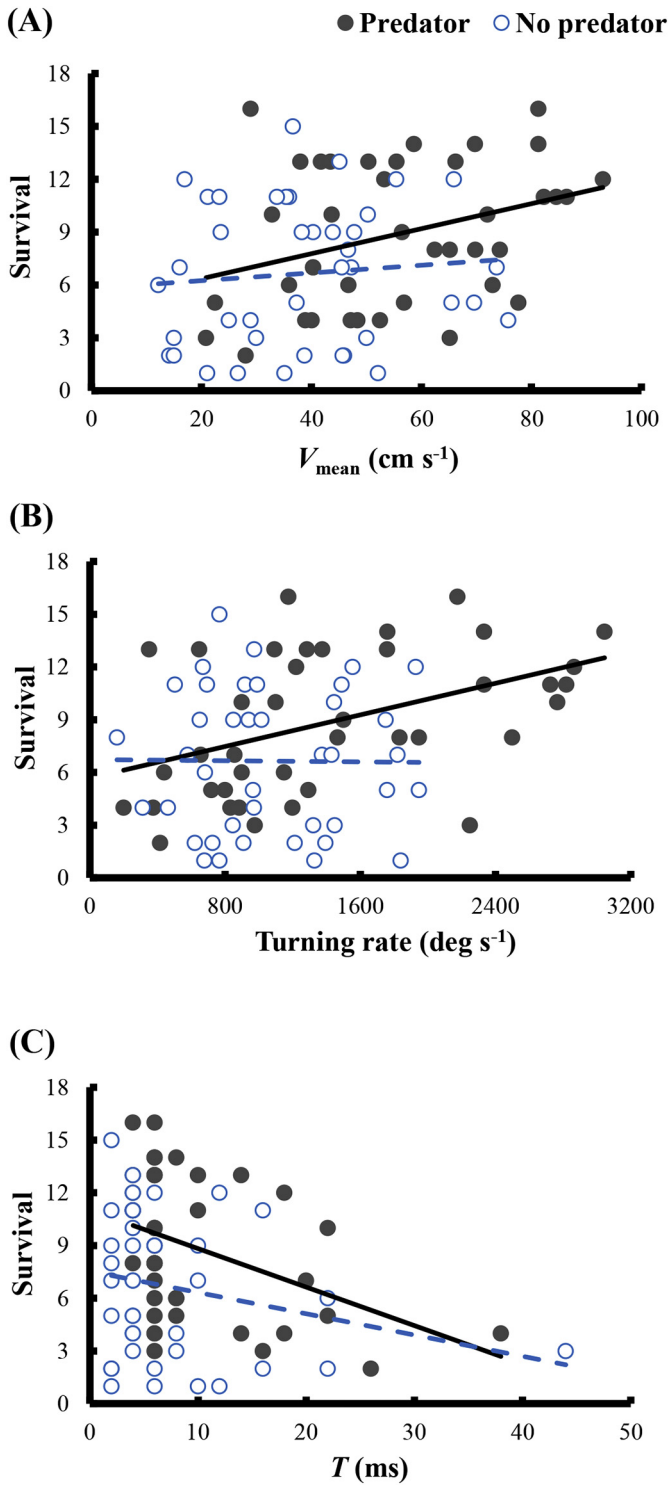

Fig. 1. Relationships between survival and mean velocity (V_{mean}, A), turning rate (B), and response latency (T, C) of fast-start performance in both the no-predator and predator groups of Chinese bream based on a Pearson correlation. Occasionally, 2 or 3 PIT tags were found simultaneously, so the rank order of the corresponding bream would be the same and the maximum value would be < 20.

respectively. v is the total volume of the respirometer (3 L) minus the volume of the fish. The maximal $\dot{M}_{O2}$ during the U_{crit} test was defined as the MMR and was used as an indicator of respiratory capability (Yan et al., 2013; Norin and Clark, 2016).

2.3.4. Survival capability under predation

After 7 d of recovery following the measurement of U_{crit}, the 80 Chinese bream were randomly divided into 4 groups to measure survival under predation. Each group contained 20 fish, with 10 fish from both the no-predator and predator groups. The 4 groups of fish were then transferred into individual tanks (280 L, length × width × height: 0.8 × 0.7 × 0.5 m, $N = 4$) with a catfish (500–600 g, fish of similar sizes were selected) to determine the survival of the Chinese bream under predation. After being eaten and digested by the catfish, the PIT tags of each Chinese bream were excreted with feces. The predation tanks were checked to collect the PIT tags excreted by the catfish every 3 h to determine the order in which the Chinese bream were eaten. The order (0–20) in which each fish was eaten was termed the survival order, and a larger order number means that the fish was eaten later and had a stronger survival capability. Sometimes, 2 or 3 PIT tags were found simultaneously, the rank order of the corresponding bream would be the same and the maximum value would be < 20.

2.4. Statistical analysis

SPSS 17 was used for data analysis. All values are presented as the mean ± se, and $P < 0.05$ was taken as the level of statistical significance. The differences in critical (MMR and U_{crit}) and fast-start (V_{max}, A_{max}, V_{mean}, turning rate and T) swimming performances and survival capability between the no-predator and predator groups were analyzed by ANCOVA, with the tank as a random factor and body mass (MMR) or length (U_{crit}, V_{max}, A_{max}, V_{mean}, turning rate, T and survival capacity) as the covariate. The relationships between critical (residual MMR and U_{crit}) and fast-start (V_{max}, A_{max}, V_{mean}, turning rate and T) swimming performance and survival of both the no-predator and predator groups were analyzed using Pearson correlations.

3. Results

3.1. Effects of predation experience on critical and fast-start swimming performance and survival

Neither the MMR ($F_{1,\ 74} = 0.384$, $P = 0.537$) nor the U_{crit} ($F_{1,\ 74} = 0.075$, $P = 0.785$) of the critical swimming capability exhibited significant differences between the no-predator and predator groups (Table 1, see detailed statistical results in Supplementary materials Table S1). The V_{max} ($F_{1,\ 74} = 6.970$, $P = 0.010$), V_{mean} ($F_{1,\ 74} = 18.324$, $P = 0.000$) and turning rate ($F_{1,\ 74} = 6.289$, $P = 0.014$) of the predator group were significantly higher than those of the no-predator group (Table 1). The survival of the predator group was significantly higher than that of the no-predator group ($F_{1,\ 74} = 7.278$, $P = 0.009$, Table 1).

3.2. Effects of predation experience on the relationships between critical and fast-start swimming performance and survival

None of the fast-start or critical swimming components exhibited a significant correlation with survival in the no-predator group ($P > 0.05$) (Fig. 1A, B, C; Table 2). However, in the predator group, both V_{mean} (x) and turning rate (x) were positively related to survival (y), and the regression equations were $y = 0.071\times + 4.932$ ($N = 40$, $R^2 = 0.112$, $P = 0.035$) (Fig. 1A; Table 2) and $y = 0.002\times + 5.680$ ($N = 40$, $R^2 = 0.198$, $P = 0.004$) (Fig. 1B; Table 2), respectively. In addition, T (y) showed a negative correlation with survival (y), and the regression equation was $y = -0.219\times + 11.02$ ($N = 40$, $R^2 = 0.162$, $P = 0.010$) (Fig. 1C; Table 2).

None of the fast-start swimming components exhibited a significant correlation with those of critical swimming in the no-predator group ($P > 0.05$) (Fig. 2A, B, C; Table 2). However, in the predator group, both V_{max} (y) and V_{mean} (y) exhibited a negative correlation with U_{crit} (x), and the regression equations were $y = -2.06\times + 268.26$ ($N = 40$, $R^2 = 0.125$, $P = 0.025$) (Fig. 2A; Table 2) and $y = -1.609\times + 161.46$

Table 2
Relationships between critical (MMR, U_{crit}) and fast-start (V_{max},A_{max},V_{mean}, turning rate,T) swimming capacity and survival under predation of juvenile Chinese bream in no-predator and predator groups based on a Pearson correlation (N = 40).

		No-predator							Predator						
		U_{crit}	V_{max}	A_{max}	V_{mean}	Turning rate	T	Survival	U_{crit}	V_{max}	A_{max}	V_{mean}	Turning rate	T	Survival
Residual MMR	r	**0.508**	−0.104	0.051	−0.060	−0.119	−0.036	0.135	0.140	0.175	−0.090	0.068	−0.017	−0.101	0.072
	P	**0.001**	0.522	0.753	0.714	0.463	0.826	0.408	0.389	0.281	0.587	0.676	0.917	0.537	0.660
U_{crit}	r		−0.087	0.057	−0.081	−0.308	−0.027	0.134		**−0.354**	−0.017	**−0.468**	−0.211	**0.317**	−0.231
	P		0.592	0.726	0.619	0.053	0.866	0.411		**0.025**	0.916	**0.002**	0.192	**0.046**	0.151
V_{max}	r			**0.475**	**0.447**	0.230	0.222	−0.207			0.256	**0.402**	0.176	−0.090	0.057
	P			**0.002**	**0.004**	0.153	0.168	0.200			0.115	**0.010**	0.278	0.579	0.728
A_{max}	r				0.289	−0.200	−0.167	0.185				0.166	−0.103	−0.013	0.037
	P				0.070	0.217	0.302	0.254				0.314	0.526	0.939	0.821
V_{mean}	r					**0.594**	**−0.539**	0.092					**0.679**	**−0.336**	**0.334**
	P					**0.000**	**0.000**	0.571					**0.000**	**0.034**	**0.035**
Turning rate	r						−0.060	−0.010						**−0.491**	**0.445**
	P						0.715	0.951						**0.001**	**0.004**
T	r							−0.235							**−0.402**
P								0.145							**0.010**

Note: The bold values indicate significant correlation between critical and fast-start swimming capacity and survival under predation of both groups ($P < 0.05$).

(N = 40, R^2 = 0.219, P = 0.002) (Fig. 2B; Table 2), respectively. Furthermore, T (y) was positively related to U_{crit} (x) in the predator group, and the regression equation was $y = 0.425\times - 18.189$ (N = 40, R^2 = 0.101, P = 0.046) (Fig. 2C; Table 2).

4. Discussion

The main objective of this study was to investigate the effect of predation experience on the relationship between fast-start swimming performance and survival under predation. We also tested the effect of predation experience on the relationship between critical and fast-start swimming at the individual level. Fast-start performance was not related to survival in the no-predator group, but a positive relationship between fast-start swimming performance and survival was found in the predator group after 20 d of predator exposure. Thus, the faster-start hypothesis is confirmed for the predation group, indicating that the recognition of and vigilance for predators achieved through predation experience can be a crucial precondition for the initiation of the fast-start escape response by prey, especially when escaping from ambush predators. Furthermore, we found no relationship between critical and fast-start swimming performance at the individual level in the no-predator group, but a tradeoff was observed between these two swimming performances in the predator group after 20 d of predator exposure. This finding may because the increased fast-start performance intensified the competition within the entire locomotion-support system (e.g., energy and the proportions of slow- and fast-twitch muscle fibers) between critical and fast-start swimming.

4.1. Effects of predation experience on critical and fast-start swimming performance and survival

Improving fast-start performance is an important strategy for fish species when escaping from predators (Walker et al., 2005), and variations in fast-start performance may be due to genetic (Langerhans et al., 2004; Domenici et al., 2008; Fu et al., 2015) or phenotypic plasticity (Fu, 2015; Liu et al., 2016). In this study, the predator group showed improved fast-start V_{max}, V_{mean}, turning rate and survival capability after 20 d of predator exposure. This improved survival capability may mainly have been due to increased fast-start escape responsiveness, maneuverability and velocity being plastic responses that result from predation experience. Different prey species may exhibit improvements in different fast-start performance components. For example, pale chub (*Zacco platypus*, from high-predation habitats) and qingbo (*Spinibarbus sinensis*, with predation experience) showed decreased fast-start response latency (Fu et al., 2015; Fu, 2015; Liu et al., 2016), while crucian carp (*Carassius carassius*, from ponds with predators) showed increased fast-start velocity, acceleration and flexibility (turning rate) (Domenici et al., 2008). The mechanisms underlying the improvements in different fast-start swimming components should be different; e.g., shortened response latency may rely on improved sensitivity of the nervous system (Turesson and Domenici, 2007; Fu et al., 2015), while velocity, acceleration and flexibility may due to variations in morphology and muscle tissue (Reidy et al., 2000; Domenici et al., 2008). In this study, the bream from the predator group were kept with catfish during the 20 d of predator exposure, and the chemical and visual alarm cues from the predated bream combined with being directly chased by the catfish may have increased the sensory sensitivity and movement (i.e., exercise) of the bream from the predator group, thus improving the fast-start performance and survival.

4.2. Predation experience underlies the relationship between fast-start swimming performance and survival

Most previous work suggests that improved fast-start performance can increase the survival capability of prey under predation (Walker et al., 2005; Langerhans, 2009b; Domenici and Kapoor, 2010), while such a relationship still requires further study. In this study, none of the fast-start components were related to survival in the no-predator group. However, both the fast-start V_{mean} and turning rate were positively related to survival, and T was negatively related to survival in the predator group after 20 d of predator exposure. This finding indicates that predation experience may help fish to recognize predators and remain vigilant (Lönnstedt et al., 2012), which may be preconditions for individuals to initiate the fast-start escape. The fish without predation experience may have been captured by predators before initiating fast-start swimming. The southern catfish is an ambush predator (Yan et al., 2015), so its prey will be captured easily by sneak attack if unfamiliar with their predator. Walker (2005) found that the fast-start performance (e.g., maximum velocity, distance traveled) of guppies (*Poecilia reticulata*) from a mixed population (most of the individuals were offspring of guppies from habitat with predators) was also related to survival capability. These results were similar to those of this study, although Walker et al. did not separately investigate the guppies without predation experience. The critical swimming components were not related to survival in either the predator or the no-predator group, and it appears that fast-start swimming would be more important for escaping from ambush predators (Reidy et al., 2000; Marras et al., 2010).

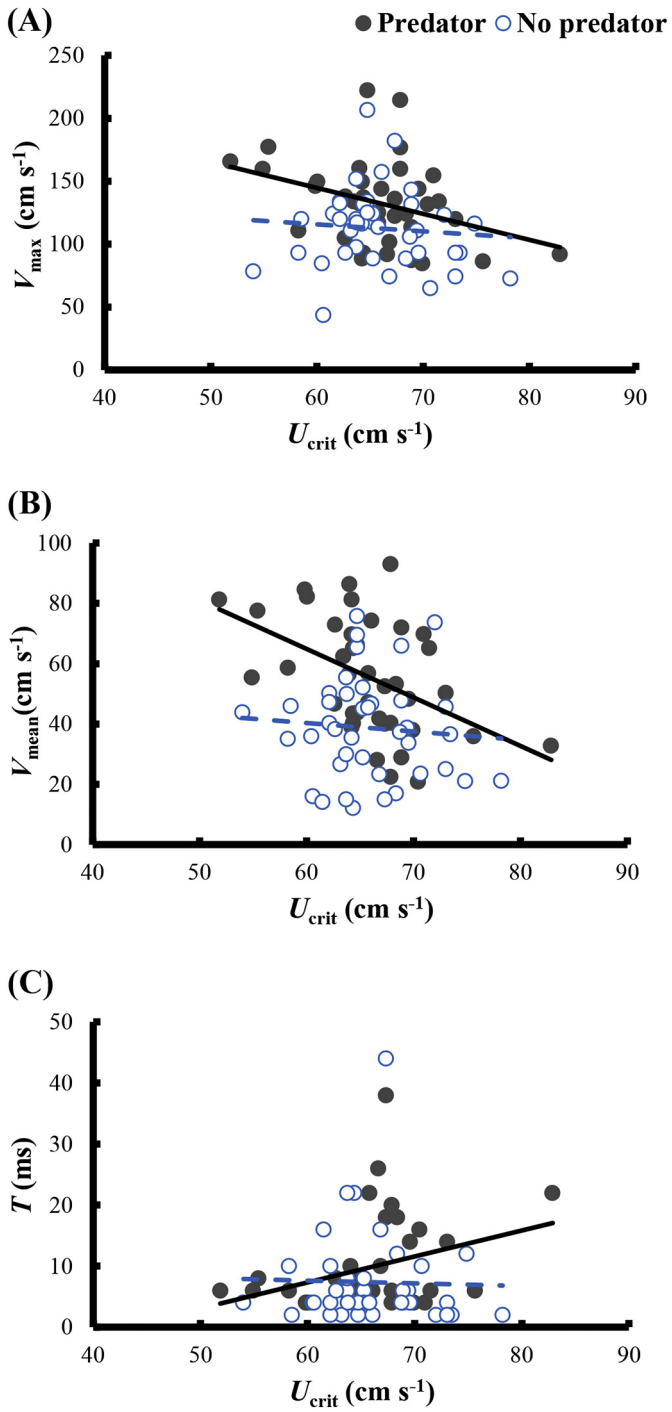

Fig. 2. Relationships between critical swimming speed (U_{crit}) and maximum linear velocity (V_{max}, A), mean velocity (V_{mean}, B) and response latency (T, C) of fast-start performance in both the no-predator and predator groups of Chinese bream based on a Pearson correlation.

4.3. Predation experience reveals the relationship between critical and fast-start swimming

In this study, we hypothesize that the relationship between critical and fast-start swimming may be context dependent. At the individual level, we found that fast-start swimming performance was not related to critical swimming performance in the no-predator group. However, the U_{crit} was negatively related to V_{max} and V_{mean} and positively related to T in the predator group after 20 d of predator exposure, although neither the U_{crit} nor the MMR of the predator group decreased. A tradeoff between critical and fast-start swimming performance was observed at the individual level after the predator exposure treatment, which may be because critical and fast-start swimming and other daily activities share the entire locomotion-support system (e.g., energy and muscle system) of fish. The fast-start performance of individual fish may be random without a predation threat because fast-start swimming is mainly used for escaping from predators (especially for the herbivorous Chinese bream) (Langerhans, 2009b; Domenici and Kapoor, 2010). When encountering a predator, each fish must adjust its physiological demands to improve its fast-start performance. Individuals with high critical swimming performance require more resources for their locomotion-support systems (e.g., greater energy consumption and proportion of slow-twitch muscle fibers) due to their higher demand for aerobic metabolism (Komi, 1984; Biro and Stamps, 2010; Dalziel et al., 2012; Dalziel and Schulte, 2012), so they may have less energy and a lower proportion of fast-twitch muscle fibers available to support improvements in fast-start performance (Komi, 1984) and thus exhibit reduced improvements in fast-start performance under the threat of predation. In contrast, individuals with low critical swimming performance in the predator group may exhibit a drastic increase in fast-start performance resulting in the tradeoff between critical and fast-start swimming at the individual level after 20 d of predator exposure.

That neither the U_{crit} nor MMR of the predator group decreased may suggest that critical swimming is also important for survival (Grorud-Colvert and Sponaugle, 2006; Fu, 2015). In addition, anaerobic metabolism may be involved in critical swimming at the end of the U_{crit} test (Nelson, 1990; Nelson et al., 1996; Reidy et al., 2000). During the U_{crit} test of the predator group, the improved anaerobic locomotion performance may compensate for the decreased aerobic locomotion performance caused by the reduced occupancy of the locomotor system. This dynamic may be why MMR was positively related to U_{crit} in the no-predator group while such a relationship disappeared in the predator group.

Conflict of interest

We declare no conflict of interest.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cbpa.2018.09.005.

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