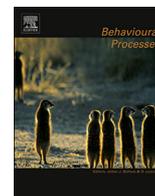




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# Aggressive behavior variation and experience effects in three families of juvenile Chinese mitten crab (*Eriocheir sinensis*)



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## ARTICLE INFO

## Keywords:

*Eriocheir sinensis*

Aggressive behavior

Family

Experience

## ABSTRACT

To assess how variable is the aggressive behavior among families (A, B, and C) and the experience effect of fighting among juvenile Chinese mitten crab (*Eriocheir sinensis*), we performed a total of 36 pairs of intrafamily and interfamily contests between three families of *Eriocheir sinensis*, qualifying and quantifying their aggressive acts and 13 pairs of winners within family and between family A and B. A table of aggression intensity was established, ranging from 1 (chasing) to 4 (intense combat). Crabs of intrafamily association performed more aggressive acts of shorter duration than interfamily, family B was more aggressive than those from families A and C: family C was the least aggressive, which is also the most morphologically distinct strain (a new strain with a red carapace). During the second fighting trial, the intensity and number of fights were significantly different to first fight conditions and also differed among families. Therefore, our results suggest that the aggressive behavior of *Eriocheir sinensis* is different among different families, and the combat experience has a significant effect on the secondary fight. This is the first report of aggressive behavior in *Eriocheir sinensis*, a reference for crab aquaculture and provides new ideas for genetic breeding work in crab selected breeding programmes. It will be possible to carry out more profound studies of the behavior of these animals.

## 1. Introduction

Fighting and aggression has received a great deal of attention over the past decades, especially in a wide range of crustaceans which with two claws as armament are more likely to fight, competing in the acquisition or defense of vital resources such as food, shelter, or access to mates (Arnott and Elwood, 2009; Clutton-Brock and Parker, 1995). Intensified aggression can cause harm to an individual and others (Jones and Norton, 2015; Mineur et al., 2003), meaning that this behavior must be carefully controlled (Jones and Norton, 2015). Thus, aggression is a behavior that may have important effects on both the ecology and aquaculture fitness of individuals. Aggressive ability and contest outcome are influenced by size (Beattie et al., 2012; Matheson and Gagnon, 2012), age, contestant, experience (Hsu et al., 2006), and other factors (Arnott and Elwood, 2009).

A fight can lead to a dominance relationship and form a social hierarchy (Chase et al., 2002). Dominance relationships are based on differences between the contenders either in intrinsic, or extrinsic factors, such as previous agonistic experiences that include winner and loser effects (Earley and Dugatkin, 2006; Khazraie and Campan, 1999). In addition, animal families play an important role in biology and

genetic breeding research, for which they have different characteristics. Therefore, different families of a species may differ in aggressive behavior and experience of fighting may alter subsequent intensity of contests; however, little is known about how family is linked with the ability to win fights (resource holding potential) or about how the experience of fighting is related to the aggressive intensity of two winners.

The Chinese mitten crab *Eriocheir sinensis* (Milne-Edwards, 1853) is a native crustacean with a long history, in view of its high nutritional value and economic value, Chinese mitten crab farming has increasingly become a booming commercial aquaculture industry in China (Yuan et al., 2017). It is widely distributed in China, however, there are few studies of mitten crab behavior, especially the fighting behavior affecting their effective farming. The juvenile *Eriocheir sinensis* of Guanghe No. 1 was selected as research materials, since such juvenile crabs are stocked at high densities in freshwater nursery ponds and always cause aggressive behaviors that adversely affect their survival rate. It was the first new strain of Chinese mitten crab bred in China. This study of the behavioral variations among them can be used to develop a base for advanced, selective breeding.

To understand the ability and intensity of the family aggressivity and the influence of the experience effects on two winners within

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<https://doi.org/10.1016/j.beproc.2019.06.002>

Received 9 December 2018; Received in revised form 11 May 2019; Accepted 1 June 2019

Available online 03 June 2019

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family and between families, we evaluate the influence of winner effects over the outcome of a fight. Two of the families (A, B) were randomly selected, one of the families (C) is a new family of breeding strains (Guanghe No. 1 with a red carapace), so that we can perform a preliminary study on the viability and aggression of family C and their differences from other families, which is important for future breeding work. The analysis of all the fights of each triad allows us to evaluate the agonistic performance of each member of the triad. Crabs that were similar in size tended to have longer or more intense fights than crabs that differed in size (Smallegange and van der Meer, 2006), and male crabs with two powerful claws are more aggressive than females (Schenk and Wainwright, 2001; Sinclair, 1977). Therefore, we chose size-matched males as experimental subjects.

## 2. Materials and methods

### 2.1. Animals and maintenance

Experiments were conducted in the Research & Development Centre, Panjin Guanghe Crab Industry Co. Ltd, in March 2018. All of the healthy male crabs (without deformity) with similar size ( $4.5 \pm 0.5$  g) were obtained from three families in the breeding workshop and isolated in individual white plastic containers (30 cm diameter, 50 cm height, ~25 L volume) for one week in the laboratory to minimize any effects of previous social experience (Ayres-Peres et al., 2011; Guiasu and Dunham, 1999). The animals were acclimated under room temperature ( $16.1 \pm 1.9$  °C) and over a photo-period of 12:12 h light/dark. We fed the individuals regularly every day with clam and stopped feeding 24 h before the experiment. Water was changed every other day during the maintenance period.

### 2.2. Preliminary experience: behavior of *Eriocheir sinensis*

We conducted two previous experiments in Panjin Guanghe Crab Industry Co. Ltd in April and July, 2017, with juvenile and adult *Eriocheir sinensis* respectively. Six families of *Eriocheir sinensis* were randomly selected, and a total of 30 groups of trials were observed for 24 h (the method was similar to that used in the formal experiment). Through experimental observation, we could understand the general rules governing the fighting behavior of crabs, which laid a foundation for our formal experiment. We also found that even without inducing factors, there would be aggressive behavior when the crabs encountered each other, and such behavior most occurred within the first 2 h of the observation period, so trials were recorded for two hours. The dominance hierarchies could be easily established especially in adult and were more stable during the period while that of the juvenile could be changed several times (see below). According to previous experimental experience and referring to previous work (Ayres-Peres et al., 2011) as standards for quantifying behavior, we developed our own scoring system for Chinese mitten crabs (Table 1).

### 2.3. Experiment I: aggressive behavior variation in three families

We chose three families of crabs recorded as A, B, and C, interfamily and intrafamily members of competitor crabs were varied in a round

stage design, resulting in six different treatments (AA, BB, CC, AB, AC, and BC). Each treatment was repeated six times, and a total of 36 paired contests comprised Experiment I. Each family was marked with a small dot in a different color (using acrylic paint) on its carapace. Each pair of crabs was moved from its respective individual container to the opposite sides of an experimental arena comprising a round stage of 30 cm diameter, to which we bound a piece of mesh at the bottom to provide adhesion for the two crabs during the fight. The two crabs were covered with two small containers, we left the individuals to acclimate for 20 min, after which we lifted the containers and left the individuals to interact for 2 h. We recorded the aggressive behavior with a digital camera (DS-2CD3T25-I5). When the experiment finished, we quickly reviewed the film footage to identify winners and losers and moved the crabs back to their respective individual containers. We recorded the number and time that each animal spent in each category of agonistic behavior and graded each interaction.

### 2.4. Experiment II: experiential effects of three families

According to the outcome of Experiment I, since all of C lost between family A v. C, only one pair of C won between family B v. C and there were four pairs of family B won between family A v. B, a total of 13 pairs in Experiment II, we matched three pairs of winners in each interfamily contest (winners of AA, BB, and CC) and four pairs between the winners of families A and B (two winners of A from A v. B and two winners of A from A v. C). After the first contest, crabs were re-isolated and after an interval of at least 24 h (Pedetta et al., 2010), here, we allowed the crabs to rest for 30 h to allow us time to deduce the winners from the footage, they were staged on the third day at the same time period as shown in Experiment I. The experimental protocols and statistical data were also the same as those in Experiment I.

### 2.5. Behavioral quantification

We had repeated measures of their aggressive behavior within each treatment. To determine the differences among families, we recorded the time each individual spent in each agonistic act, then calculated the total and mean duration of the fighting acts; we also counted the number of the fights during the filmed period (the bout). The bout was deemed to have been initiated when one individual approached the opponent and the opponent did not flee and was deemed to have finished when one fled and did not interact for five seconds or more, or when they backed away from their opponent (Ayres-Peres et al., 2015). To determine aggression levels of each species, agonistic acts were given scores from 1 (without physical contact, such as approaching and chasing) to 4 (intense aggressive acts, such as unrestrained use of the claw; Table 1), and the individual that won most bouts was deemed the winner whereas the retreating animal was considered the loser of the fight and became the subordinate (Horner et al., 2008). The same researcher (Li Y.) analyzed all videos to avoid biasing the results that may be caused by different observers being used (Ayres-Peres et al., 2015).

### 2.6. Statistical analyses

We used SPSS 21.0 software for all statistical analyses. All data were

**Table 1**  
Definition of scores of aggression intensity shown by juvenile *Eriocheir sinensis*.

Score	Behavior	Definition
1	Approaching and chasing (Without physical touch)	One approaching or chasing another around the area without fighting actions.
2	Slightly physical contact	Touching the opponent with walking leg or climb on the back without fighting actions. The subordinate avoiding the dominant crab and quickly retreating.
3	Fight each other with chelae	Attacking each other with claw to claw, touching and hitting with chelipeds, finally the loser struggled to escape.
4	Intense combat	Chelae used to pull, hold, and catch the opponent, mount the body, and turn over the opponent, a fierce fight.

checked for normal distribution (Shapiro-Wilk's test) and the homogeneity of the variance (Levene's test). We log-transformed ( $\log(x + 1)$ ) these data to achieve homoscedasticity and normality. The variations of families and their interactions with different levels were analyzed by using one-way ANOVA and two-way ANOVA. The results were expressed as mean  $\pm$  standard error (SE).

### 3. Results

#### 3.1. Description of the behavior

Similar behavior was observed during agonistic interactions, we chose one of the crabs as the center crab (usually the dominant one), and the other one as the opponent. The *Eriocheir sinensis* showed a fighting behavior that mainly involved the use of two chelipeds. The combats were initiated by an approach, progressing from brief physical contacts with walking legs to touch the carapace or the opponent's walking legs, but the opponent would keep still or move away, then it would climb over the back of the opponent, or touch conversely, these acts were repeated one-to-three or more times, then an intense combat began. They would use their strong claws to touch, push, grasp, clamp, or hold the opponent. After one-to-three bouts, the dominant-subordinate levels were established and shown to be relatively stable over time, but there were also a total of six pairs of crabs experiencing a hierarchy reversal in families A and B which also happened to crayfish, *Procambarus clarkii* (Horner et al., 2008). The dominant crab opened its claw and walking legs and stayed in the middle or walked around freely in the container, while the subordinate stayed close to the wall of the container with appendages folded. As the time went by, their vigor decreased. The subordinate could tolerate the opponent climbing up and down on its body without any activity.

#### 3.2. Aggressive outcome of experiment I

Considering the total sum of interactions with which each family achieved competitive dominance, we observed that in 44.1% and 89.9% of encounters (A v. B and A v. C, respectively), family A established a dominant position, while in 55.9% and 88.8% of encounters (B v. A and B v. C, respectively) family B established a dominant position (Fig. 1a). In addition, six pairs of outcomes have been analyzed, the winning probability of family A is 33.3% v. family B, 100% v. family C, the winning probability of family B is 66.7% v. family A, 83.3% v. family C (Fig. 1b). The dominant crab who initiated a contest won most such contests (inning probability, 80%).

There were no significant differences in latency period among families of *Eriocheir sinensis* ( $p > 0.05$ ; Fig. 2a). In the two hour-long contest, family B had more bouts of fighting ( $p < 0.05$ , Fig. 3a) and long durations during the fight of intrafamily and interfamily members ( $p = 0.063$ , Fig. 4a), the aggressiveness of interfamily members were similar ( $p > 0.05$ ). In addition, we detected the intensity differences (scores) in three families of crabs and their aggression, family A was lower than other families while family B reached the maximum score ( $p < 0.05$ , Fig. 5a), the final score was recorded as the total number of points scored in each level of fight.

The number of contests of each intensity of physical interactions varied separately with crab family (Fig. 6a). There was a higher proportion of contests with weak physical interactions (level 1) and lower proportion of contests with slight physical contact (level 2) in family C compared to family A ( $p < 0.05$ ), whereas the frequency of strong physical contact (levels 3 and 4) did not differ by family ( $p > 0.05$ , Fig. 6a).

#### 3.3. Aggressive outcome of experiment II

The winning experience effect is different in different families. The latency period was decreased between winners, but had no significant

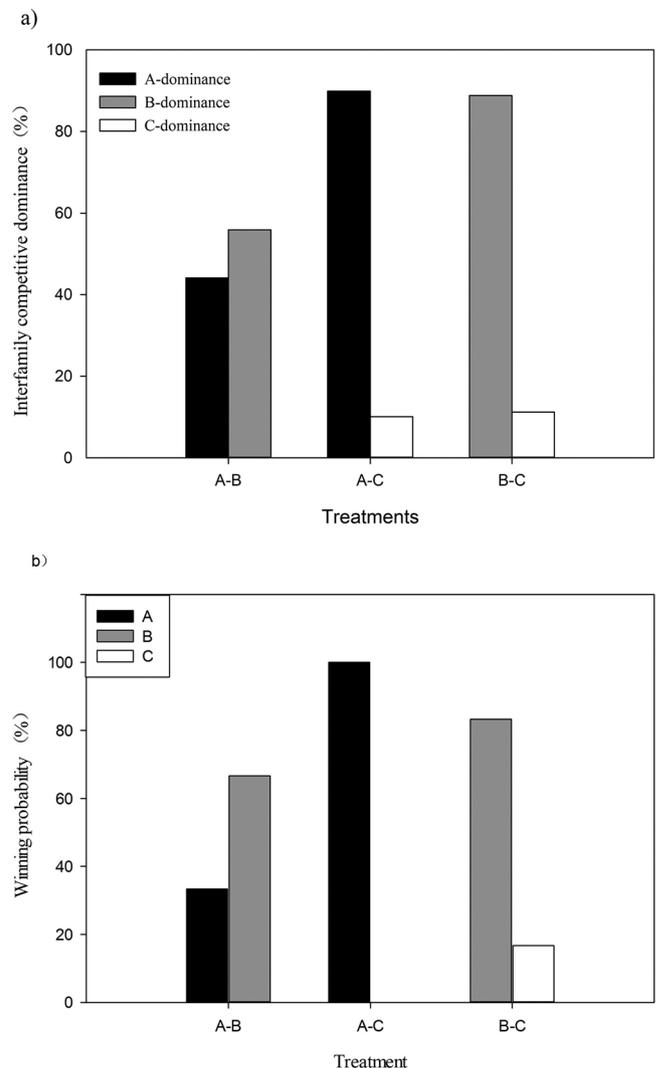


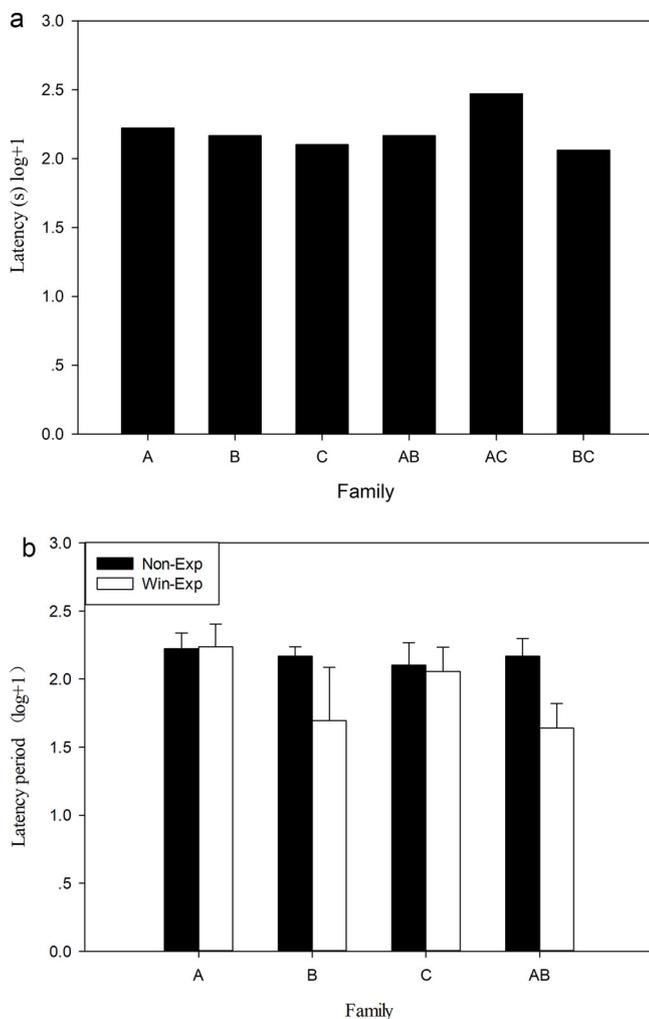
Fig. 1. (a) Frequency of dominant responses in two families of *Eriocheir sinensis* when subject to confrontations with opponents, and (b) winning probability for two families.

difference therein (Fig. 2b). Shorter latencies before starting a fight indicate greater boldness for winner crabs. The total number of fighting acts (Fig. 3b) and aggression scores (Fig. 5b) were significantly greater than the first time but were of shorter duration in family A (Fig. 4b,  $p < 0.05$ ), whereas all indicators were increased in family C ( $p > 0.05$ ), similarly in family B and family A v. B, only aggression scores were decreased in family A v. B (Fig. 4b,  $p < 0.05$ ).

In the winning family, there was also a higher proportion of contests at level 1 ( $p < 0.01$ ) and a lower proportion of contests in level 2 ( $p > 0.05$ ) in family C compared to family A, and the frequency of strong physical contact (levels 3 and 4) did not differ across families ( $p > 0.05$ , Fig. 6b). In addition, the proportion of contests at the four levels did not differ between families with no experience and with winning experience ( $p > 0.05$ ).

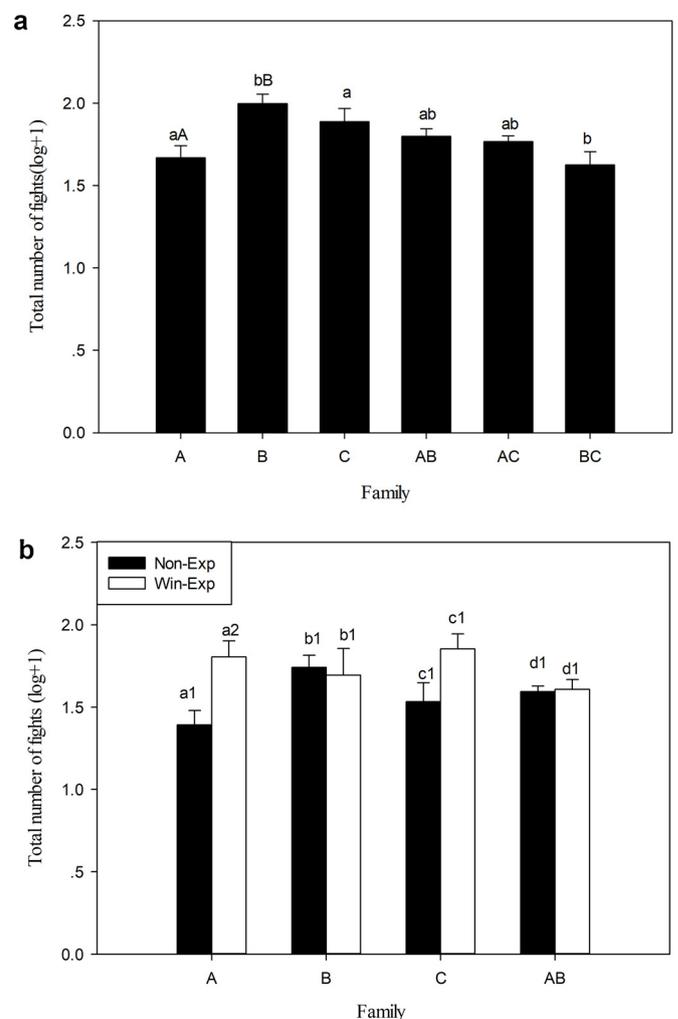
### 4. Discussion

The present study was the first to investigate the aggressive behavior variation among three families of juvenile *Eriocheir sinensis*. The juvenile *Eriocheir sinensis* rarely engages in intense combat, and is easily subjected to dominant hierarchy reversal, a decline in both the number of fights and their duration, which usually accompanies the establishment of the dominant-subordinate relationship (Guiasu and Dunham,



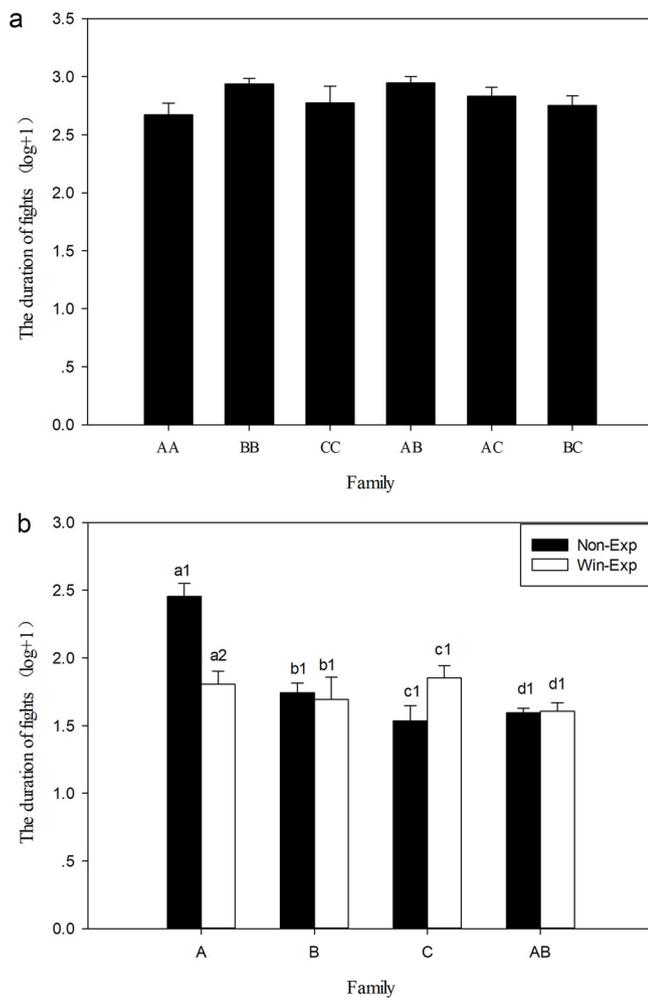
**Fig. 2.** Latency of crabs before starting a fight for the first time: (a) three families in six treatments within two hours. (b) Both crabs with winning experience (white bars □) and crabs with no-experience in Experimental I (black bars ■) within one hour.

1997; Söderbäck, 1991), indicating that this relationship was established fairly quickly, usually within the first 10-min period during each contest as reported in crayfish (Guiasu and Dunham, 1999). Several studies show that individuals exhibit consistently distinct behavior or “personality” types in many taxa (Conrad et al., 2011; Wolf et al., 2008), such as cyprinid fish (Pang et al., 2011) and crayfish, in two closely related crayfish species, *Cambarus robustus* behaved more aggressively toward *Cambarus bartonii bartonii* (Lynas et al., 2007). In three taxa of *Aegla*, the competitive hierarchy was dominated by *A. abtao*, followed by both populations of *A. araucaniensis*. *A. denticulata* was always the subordinate species (Parra et al., 2011). In the present study, we found that family B was dominant over families A and C between size-matched individuals (Fig. 1): the total number of fights and sum of aggression scores were significantly higher in family B. Family C generally concentrated on low-intensity attacks (level 1), and family A concentrated on moderate-intensity attacks (levels 2 and 3) while family B was evenly distributed (Fig. 6a). What is worth mentioning is that the aggressiveness of family C (which is a new strain of Chinese mitten crab in red shell with gentle characteristics) was strong when it competed intrafamily but become weak and lost all bouts with members of families A and B. These are models in which each contestant only has information about its own abilities or state and fails to gather information about its opponent, and the actions of the opponent do not inflict costs, although both opponents incur a cost from their



**Fig. 3.** The total number of fights (log + 1) of (a) three families in six treatments within two hours. Different letters represent a significant difference ( $p < 0.05$ ), upper case letters represent an extremely significant difference ( $p < 0.01$ ). (b) both crabs with winning experience (white bars □) and crabs with no-experience from Experimental I (black bars ■) within one hour. Numbers indicate significant differences within the experimental groups ( $p < 0.05$ ). Data are expressed as mean  $\pm$  standard error (SE).

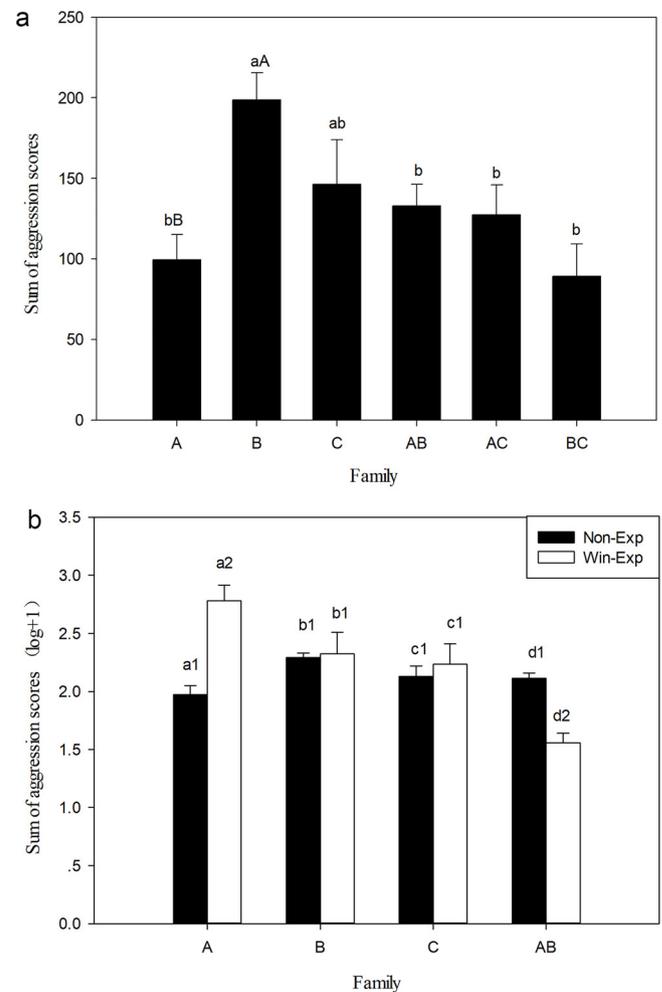
own actions. In this scenario, rivals persist purely in accord with their own RHP such that weaker rivals tend to reach their limits and give up first. This strategy is termed “self-assessment” (Arnott and Elwood, 2009). Such differences in fighting behavior lie in the interacting effects of the environment and genetic (Damsgård and Huntingford, 2012). For example, in rainbow trout, *Oncorhynchus mykiss*, raised in different social group sizes, will have different levels of aggressiveness (Sloman and Baron, 2010): however, interactions between conspecifics early in life have the potential to shape phenotypic differences between individuals and these changes in phenotype may subsequently be passed to future offspring (Tamilselvan and Sloman, 2017), strains of Siamese fighting fish (*Betta splendens*) selectively bred for cockfight-like contests are more aggressive than wild-type fish in pairwise interactions with live opponents (Verbeek et al., 2007). The existence of inherited differences in aggressiveness among cultured fish species offers the possibility of selective breeding for levels of aggression that are appropriate for fish culture, for whatever purpose (Damsgård and Huntingford, 2012) and so that in *Eriocheir sinensis*. In this study, three families of *Eriocheir sinensis* were raised in similar environment, so it may depend on genetic factors. Comparisons of difference among families in behavior offer powerful insights into the underlying genetic



**Fig. 4.** a The duration of fights ( $\log + 1$ ) of (a) three families in six treatment within two hours. (b) Both crabs with winning experience (white bars  $\square$ ) and crabs with no-experience from Experiment I (black bars  $\blacksquare$ ) within one hour. Numbers indicate significant differences within the experimental groups ( $p < 0.05$ ). Data are expressed as mean  $\pm$  standard error (SE).

mechanisms and overlying selective factors that shape interactions between different types of behavior.

The effect of winning experience on aggressive behavior has been well established among fish (Hsu and Wolf, 2001), shrimp (Bergman et al., 2003), and crabs (Dodson and Schwaab, 2001). In the literature concerning experiential effects based on the outcome of a subsequent contest, overwhelming majority of studies reported individuals with a winning experience will increase their aggressiveness and appear to have an advantage against their naive opponent (Hsu et al., 2006; Huang et al., 2011); but information about the winning effect between two winners is limited, and the effect is not as significant as the effect of other experience, which make it even harder to examine the influence of winning experience on two winners. Measuring different aspects of behaviors can lead to different conclusions, contest duration and intensity were found to be better indicators of the winner effect (Huang et al., 2011), however, in the present study, fighting frequency and intensity were found to be more reliable than contest duration; in family A and C, they showed a higher frequency and intensity of fights, while family B and family A v. B only showed a shorter latency before initiating a fight with winning experience to prefight. Experiences were usually hypothesized to influence how the contestants assessed their fighting ability and thus their fighting costs in subsequent contests (Beaugrand et al., 1991; Hsu and Wolf, 1999), which is termed resource holding potential (RHP) (Parker, 1974). In this assessment model, the



**Fig. 5.** a Sum of intensity levels (1 to 4) of fights of (a) three families in six treatments within two hours. Different letters represent a significant difference ( $p < 0.05$ ), letters in capitalization represent an extremely significant difference ( $p < 0.01$ ). (b) Both crabs with winning experience (white bars  $\square$ ) and crabs with no-experience from Experiment I (black bars  $\blacksquare$ ) within one hour. Numbers indicate significant differences within the experimental groups ( $p < 0.05$ ). Data are expressed as mean  $\pm$  standard error (SE).

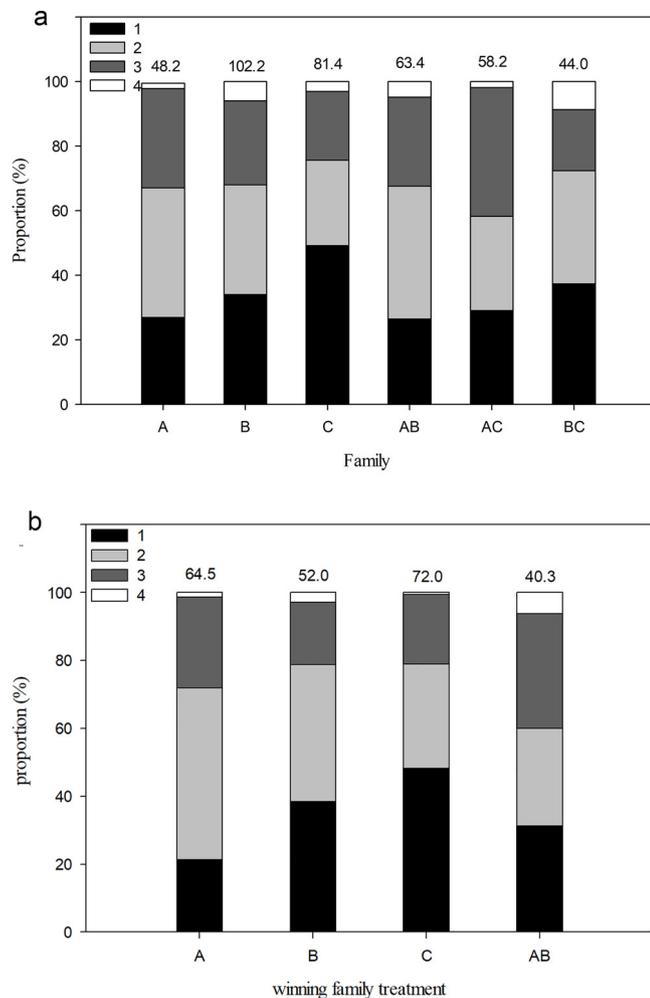
contestants gradually assess each other's true fighting ability and decide whether to escalate the contest or not; one of the winners may alter its actual fighting ability and retreat to reduce energy cost and the risk of injury, then quickly terminate the fight. Even if those with winning experiences become more aggressive and actively challenge their naive opponents, they may not be able to win as the opponent may escalate the contest.

## 5. Conclusions

Overall, in intrafamily bouts, family B was ranked as a highly aggressive family, followed by family C and family A; whereas in interfamily bouts, family B was also ranked as a highly aggressive family, then family A, with the poorest being family C. The winning experience of two winners had a significant positive effect on the frequency and intensity of contests, which also differed between families. Furthermore, behavioral variation in the families of *Eriocheir sinensis* may facilitate further breeding work.

## Author contributions

Yi Li and Xiaodong Li designed the study and wrote the manuscript;



**Fig. 6.** Standardised proportion (error bars not shown for clarity) of contests between families assigned to each for degrees of physical interactions (from 1 to 4). a) Three families in six treatments within two hours. (b) Both crabs with winning experience within one hour. Values above bars represent the mean number of contests per trial.

Yi Li, Qiuyue Jiang, and Sining Fan performed the experiments; Na Sun and Yan Zheng assisted in crab collection and cultivation.

### Competing financial interests

The authors declare no competing financial interests.

### Acknowledgement

This study was financially supported by the Breeding Public Relations Programme of Guanghe (Grant no. 2017001) and the Research Start Plan for High Level Talents of Shenyang Agricultural University (No. 880416005). We thank Panjin Guanghe Fisheries Co. Ltd, for providing the crabs.

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