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Male-Female Interactions for the Expression of Phenotypic Traits and Behavioral Performance of the Male Giant Freshwater Prawn (*Macrobrachium rosenbergii*)

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ABSTRACT

The present study explored the effects of male-female interactions on the behavior and phenotypic expression of giant freshwater prawn *Macrobrachium rosenbergii*. Juvenile male (♂) and female (♀) prawns were randomly assigned into three treatments having different M and ♀ sex ratios and stocking densities such as T_1 - only ♂ (1, 3 and 5); T_2 - single ♂: multiple ♀ (1:1, 1:3 and 1:5) and T_3 - multiple ♂: single ♀ (1:1, 3:1 and 5:1). Results showed that males in 1♂: 1♀ occupied significantly more territory (P<0.05) than 1♂, while, males in 5♂ treatment showed significant territory occupation (P<0.05) than males in 1♂: 3♀, 1♂: 5♀ and 5♂: 1♀. In female choice trials, males kept without females (1♂, 3♂ and 5♂) were chosen by the test females significantly (P<0.05) rather than males reared with females in different ratios. The phenotypic analysis revealed that males in 1♂:1♀, 1♂: 3♀ and 5♂: 1♀ treatments were significantly larger (P<0.05) than males in 3♂ treatment. The analysis also showed that males in the 5♂ treatment had significantly longer 2nd chelate-leg (P<0.05) than males in the 3 ♂: 1 ♀ treatment. This study would provide some baseline data for this carnivorous crustacean, which can be successfully cultured by maintaining the sex ratio.

INTRODUCTION

In animals, males often possess multiple secondary sexual traits which can serve as signals to females as well as rival males **(Candolin, 2003)**. Multiple signals could evolve due to individual females exhibiting multiple, independent preferences **(Brooks & Couldridge, 1999)** and/or because spatially or temporally heterogeneous environments favor different cues **(Bro-Jørgensen, 2010)**, potentially reinforcing an overall signal of quality. Signals and the information they deliver are likely to alter with age, size, reproductive experience and the environmental context **(Candolin, 2003)**. Moreover, different cues could also be aimed at different recipients as they can function both agonistically to convey a male's prowess to rivals, and sexually to convey his phenotypic or genetic information to potential mates **(Berglund *et al*., 1996)**.

Like different animals and other fishes, most crustaceans also show competition for mating especially among the males. The aggressive and dominant males win over less aggressive and subdominant males. The male reproductive success depends on male-male competition and aggression. The individuals who are at a competitive disadvantage sometimes adopt an entirely different group of reproductive behaviors **(Soundarapandian *et al*., 2008)**.

The giant freshwater prawn (*Macrobrachium rosenbergii*) is an important aquatic crustacean species which is mostly distributed in the tropical and subtropical regions. Freshwater prawns are abundant in the south-southeast Asia and Asia-pacific regions. Commercial culture of freshwater prawn in Bangladesh started in early 1990s and has become one of the top seven export countries in the world **(Ahmed, 2001)**. The major giant freshwater prawn producing countries in Asia are Bangladesh, China, India, Myanmar, Thailand and Vietnam **(Alam & Islam, 2014)**. The total global production of giant freshwater prawn was 234.4 thousand ton in 2018 of which only Bangladesh produced 5.16 thousand ton, which was the world's second largest production **(FAO, 2019)**. Although this sector is expanding rapidly, sustainability of this industry is currently threatened because of larval scarcity, diseases, low production efficiency and vulnerability of farmed stocks and climate change issues **(Thanh *et al*., 2009; Hooper *et al*., 2020; Jamal *et al*., 2021; Mathew *et al*., 2021).**

Growth of individual fish within a population is often highly variable **(Sissenwine, 1984)**. Variation in growth is an important component not only for individual's fitness but also for good reproductive output and survival. There are various causes for this growth variability including genetic, social and environmental factors **(Huang *et al*., 2021; Milla *et al*., 2021; Perera *et al*., 2021)**. Considering these factors, *M. rosenbergii* is particularly an interesting species with respect to variation in growth and reproductive performance **(Karplus & Barki, 2019; Ibarra & Wehrtmann, 2020; Li *et al*., 2021)**.

Despite the growth of this species, a number of issues are important for its farming in Bangladesh including production technology, stocking density, socio-economic and environmental aspects **(Hossain & Islam, 2006; Kunda *et al*., 2009; Ahmed *et al*., 2013)**. All of these issues are important parameters for sustainable aquaculture of this species. The primitive concept of *prawn* culture states that all male population yield better outputs than mixed sex or all-female culture **(Kunda *et al*., 2008)**. Another concept is that as stocking density increases, the increase of total yield is normally being expected. However, a corresponding increase of non-marketable prawns in the harvested population due to the decrease in mean weight is the most commercial disadvantage of this species **(Ranjeet & Kurup, 2002; Kutty & Kurup, 2017)**.

As far as genetic diversity is concerned, generally the sex ratio of prawn's brood is 1:1 **(Thanh *et al*., 2009)**. But at this moment in Bangladesh, the broods are not being recycled in the hatchery. The post-larvae (PL) produced in the hatchery are used only for grow out as table prawn. All the brood banks collect PL from rivers for stocking in the brood pond. In this case, considering the economics of brood rearing, it is better to stock 1 male: 3 females. But the males are territorialistic in nature, and therefore, the females may get more access to feed if the number of males is kept low. For spawning one male is sufficient for three females. There is no optimum stocking density in the outdoor culture of prawn. The stocking density depends on several factors such as water quality, presence or absence of aerators, presence or absence of artificial shelters and overall management **(Alam & Islam, 2014)**. Considering the conditions, farmers maintain 2:1 to 3:1 or even 5:1 of female: male sex ratios in their brood banks **(Kunda *et al*., 2008)**. As a result, all males will get the chance to find out their potential mates in order to increase genetic variability of the seeds. In addition, four social mechanisms are controlling factors for growth variation such as direct competition for food, appetite suppression in subordinate individuals, decreased food conversion efficiency and increased motor activity **(Karplus & Barki, 2019)**.

Considering the above-mentioned issues, the present study was carried out to investigate how male-male and male-female interactions can affect the expression of males' different phenotypic traits using the giant freshwater prawn as a model species. This study further observed males behavior under male-male competition and male-female interaction. The knowledge obtained from this study may provide a basis for the establishment of a practically successful culture protocol to simplify management practices in different culture phases of this commercially important species.

MATERIALS AND METHODS

Species collection and acclimatization

A total of 165 hatchery produced juveniles of giant freshwater prawn (*M. rosenbergii*) having same size (9.77±0.33 cm) and age (around 3 months) were collected from the same batch, and transported in oxygenated poly bag to the Wet Fish laboratory of Fisheries and Marine Resource Technology (FMRT) Discipline, Khulna University, Bangladesh. These juveniles were transferred into a couple of large glass aquarium (50cm × 29cm × 30cm) with appropriate facilities to acclimatize them for two days before starting the experiment.

Water quality management

The hatchery water mixed with near-by pond water was used for rearing of juveniles. Each aquarium (20cm×30cm×30cm) was fitted with continuous aeration and covered with a net to avoid the escape of any juveniles. About half of the water was removed by siphoning every alternative day to clean the faces and uneaten food. Adhered dirt inside the aquarium walls was also cleaned once a week. During the experimental period, water temperature, pH and dissolved oxygen (DO) of water was monitored once a week using YSI Professional plus water quality meter.

Feeding

Juveniles were fed with a commercial prawn pellet (Quality Feeds Limited, Bangladesh) containing 35% crude protein at stocking that was reduced to 30% for the last 4 grow-out weeks. Feed was applied at 3-4% of the total body weight of stocked juveniles and supplied twice a day during morning (around 9 am) and at evening (around 7 pm).

Experimental design

Male (♂) and female (♀) were sorted out and then randomly assigned into three treatments including T_1 - Only male (1, 3 and 5♂); T_2 - single ♂ : multiple ♀ (1 : 1, 1 : 3 and 1 : 5) and T_3 - multiple ♂ : single ♀ (1 : 1, 3 : 1 and 5 : 1). The male-male interactions in different densities were maintained in T_1, while male-female interactions were allowed in T_2 (one male with different number of females) and T_3 (one female with different number of males). This design allowed males to compete with rival males and interact with females at different sex ratios. Thus, the design also facilitated to explore the effects of different stocking densities on their interactions. Each treatment of different sex ratios had three replications, and they were kept separately in the same sized tanks with same facilities. The experiment was carried out until the sexual maturity of males (three months) and observed different phenotypic traits and behavioral approaches of these experimental males. The studied males and females were observed periodically to detect the sign of their sexual maturation by observing their phenotypic changes such as body color, development of appendages and behavioral traits, etc. **(Kuris *et al*., 1987; Barki *et al*., 1992)**.

Observation of behavioral performances

After the three months of rearing, each experimental male was transferred to a same sized behavioral tank in order to find its dominancy attitude by keeping it for 20 minutes with every male of other treatments separately. A female was also released into the tank with those rival males. First, they were given 5 minutes to adjust and acclimatize with the behavioral tank condition. Then some behavioral performances were recorded through eye observation including fighting score (how many times one male attacks the rival one within 20 minutes within 30 minutes), territory occupation (when they are fighting, a male moves towards and pushes the rival male to a corner of the tank to occupy the entire space (i.e. territory)), and female's choice (when a male between two competitive males occupies most of the territory of behavioral tank; the female mostly prefers this territory winner for her mating partner). During this behavior, the winner male encircles the female with his second pereiopods approaching her for mating and evicts the other male for mate guard.

Phenotypic traits measurement

After finishing the behavioral observation, each male was carefully taken to measure its total length (from tip of rostrum to tip of telson), carapace length (from posterior margin of orbit to posterior edge of carapace), 2^{nd} chelate leg's length (longest and colorful leg) and detected its color. The lengths of blue and orange portion of 2^{nd} chelate leg were also measured. The lengths were measured by following **Rebello *et al*. (2014)** to the closest 0.1 cm using a measuring board.

Statistical analyses

All analyses were performed using 'RStudio' version 4.0.2 **(R Development Core Team, 2020)**. The descriptive statistics (means, SEs, etc.) were calculated with 'Describe-By' function using the 'psych' package **(Revelle, 2017)**. Both behavioral traits and phenotypic traits had small sample sizes. Therefore, the Fisher's exact test of independence was employed using 'Fisher test' function for behavioral data analysis which allowed for small sample sizes to see whether the proportions of one nominal variable were different depending on the value of the other nominal variable **(McDonald, 2014)**. To explore the phenotypic trait variation between two competitive groups; the Wilcoxon signed-rank test was applied using 'Wilcox test' function for the paired t–test, where the population means are assumed to non-normally distributed **(McDonald, 2014)**.

RESULTS AND DISCUSSION

The Fisher's exact test revealed no males of a particular treatment achieved significant score during the fighting performance test to defeat the opponent males **(Table 1)**. During the territory occupation performance test, it was observed that 1♂:I♀ occupied more territory than 1♂ (P<0.05). Similarly, more territory was occupied by 1♂:3♀ (P<0.05), 5♂:1♀ (P<0.05) and 1♂:5♀ (P<0.05) than 5♂. Except these males, others did not show significantly variable performance during the territory occupation test (Table 1). It was found that female chose significantly 1♂ rather than male in 3M and 1♂:1♀ treatments (P<0.05). Similarly, 3M were more chosen by females rather than male in 1♂:1♀, 1♂:3♀ and 1♂:5♀ (P<0.05). The findings also revealed 5♂ were mostly chosen by females than males in 1♂:1♀ (P<0.05). All the other males were not significantly preferred by the females as their mating partners during this test (Table 1).

Table 1. Behavioral performances between two competitive males of different treatments

Competitive males of different treatments	**Fighting score**		**Territory occupation**		**Females' choice**	
	(Mean±SE)	*P*	(Mean±SE)	*P*	(Mean±SE)	*P*
1M vs. 3M	16.25±3.15	0.43	1.25±0.25	0.49	2.00±0.00	***0.03***
	20.0±4.08		1.75±0.25		1.00±0.00	
1M vs. 5M	8.75±3.75	0.06	1.75±0.25	0.49	1.75±0.25	1
	13.75±1.25		1.75±0.25		1.75±0.25	
1M vs. 1M : 1F	8.75±1.25	0.09	1.00±0.00	***0.03***	2.00±0.00	***0.03***
	21.25±2.39		2.00±0.00		1.00±0.00	
1M vs. 1M : 3F	22.50±2.50	0.09	1.75±0.25	0.49	1.75 ±0.25	0.49
	19.75±1.03		1.75±0.25		1.75±0.25	
1M vs. 1M : 5F	15.75±6.43	0.2	1.75±0.25	0.49	1.75±0.25	1
	20.0±3.54		1.75±0.25		1.75±0.25	
1M vs. 3M : 1F	20.75±4.71	0.77	1.50±0.29	1	1.75±0.25	0.49
	18.75±2.39		1.50±0.29		1.25±0.25	
1M vs. 5M : 1F	15.00±2.04	1	1.50±0.29	1	1.75±0.25	0.49
	15.00±3.54		1.50±0.29		1.25±0.25	
3M vs. 5M	25.50±2.63	0.09	1.75±0.25	0.49	1.75±0.25	0.49
	22.50±2.50		1.25±0.25		1.25±0.25	
3M vs. 1M : 1F	21.25±5.54	1	1.25±0.25	0.49	2.00±0.00	***0.03***
	25.00±4.56		1.0±0.00		1.0±0.00	
3M vs. 1M : 3F	20.00±4.08	1	1.75±0.25	0.49	2.00±0.00	***0.03***
	12.50±3.23		1.25±0.25		1.0±0.00	
3M vs. 1M : 5F	22.50±2.50	0.09	1.75±0.25	0.49	2.00±0.00	***0.03***
	16.75±6.10		1.25±0.25		1.00±0.00	
3M vs. 3M : 1F	20.00±6.12	0.43	1.25±0.25	0.49	1.75±0.25	0.49
	26.25±3.75		1.75±0.25		1.25±0.25	
3M vs. 5M : 1F	26.25±6.25	1	1.75±0.25	0.49	1.75±0.25	0.49
	23.00±3.63		1.25±0.25		1.25±0.25	

5M vs. 1M : 1F	30.75±4.97 22.50±3.23	1	1.50±0.29 1.50±0.29	1	1.75±0.25 1.25±0.25	0.49
5M vs. 1M : 3F	21.25±3.75 10±2.89	0.43	2.00±0.00 1.0±0.00	***0.03***	2.00±0.00 1.0±0.00	***0.03***
5M vs. 1M : 5F	32.50±8.29 31.25±14.91	0.657	2.00±0.00 1.0±0.00	***0.03***	2.50±0.29 1.0±0.00	0.49
5M vs. 3M : 1F	18.75±7.18 20.00±3.54	0.49	1.25±0.25 1.75±0.25	0.49	1.25±0.25 1.75±0.25	0.49
5M vs. 5M : 1F	35.00±3.54 20.00±4.56	0.66	2.00±0.00 1.0±0.00	***0.03***	1.75±0.25 1.0±0.00	0.49

M indicates 'male' and F indicates 'female'. Significant *P*-values are marked in bold and italic fonts.

Phenotypic traits

At the end of the experiment, it was found that males in 1♂: 1♀, 1♂: 3♀ and 5♂: 1♀ had significantly ($P<0.05$) larger total length than that of 3♂. Except these males, others were not significantly variable in terms of total length (Table 2). The Fisher's exact test revealed no significant variation among the males of different treatments in terms of carapace length (Table 2). The results displayed that 5♂ possessed significantly larger 2nd chelate leg than males in 3♂: 1♀ treatment ($P<0.05$). Except these males, other groups did not show any significantly larger 2nd chelate leg at the end of the experiment (Table 2). The Fisher's exact test disclosed that male in 1♂: 5♀ had significantly more blue color in their 2nd chelate leg than that of 1♂ ($P<0.05$), while no other groups had significant blue color in their 2nd chelate legs at the end of the study (Table 2). The findings also revealed no males significantly possessed orange color in their 2nd chelate leg at the end of the experiment (Table 2).

Table 2. The outcomes of Wilcoxon t-test showing the phenotypic variation among males of different treatments. Here, M indicates 'male' and F indicates 'female'. Values are given mean ± standard error (SE). Different superscript letters indicate the significant variation in a trait among different treatments ($P<0.05$).

Phenotypic traits	1♂	3♂	5♂	1♂ : 1♀	1♂ : 3♀	1♂ : 5♀	3♂ : 1♀	5♂ : 1♀
Total length (cm)	10.52±0.00^{ab}	10.48±0.39^{a}	12.10±0.75^{ab}	12.09±0.47^{b}	11.61±0.14^{b}	11.41±0.33^{ab}	11.03 ±0.36^{ab}	11.85±0.36^{b}
Carapace length (cm)	2.80±0.02^{a}	2.75±0.04^{a}	2.91±0.14^{a}	2.88±0.10^{a}	2.81±0.10	2.98±0.08^{a}	2.76 ±0.10^{a}	2.75±0.08^{a}
Total chelate-leg length (cm)	0.88±0.11^{ab}	1.04±0.33^{ab}	1.52 ±.25^{b}	0.90±0.32^{ab}	1.02 ±0.31^{ab}	1.08±0.21^{ab}	0.66 ±0.24^{a}	1.00±0.27^{ab}
Length of blue chelate (cm)	0.56±0.06^{a}	1.01±0.34^{ab}	1.07 ±0.29^{ab}	1.00±0.21^{ab}	1.37±0.26^{ab}	1.37±0.10^{b}	1.00 ±0.12^{ab}	1.30±0.14^{ab}
Length of orange chelate (cm)	0.32 ±0.05^{a}	0.54±0.32^{a}	0.25 ±0.11^{a}	0.19±0.11^{a}	0.05 ±0.03^{a}	0.11±0.06^{a}	0.15 ±0.09^{a}	0.32±0.17^{a}

DISCUSSION

Alternative mating strategies have primarily focused on behavioral or developmental differences among individuals in many fish species including arctic charr **(Sigurjónsdóttir & Gunnarsson, 1989)**, freshwater prawn **(Karplus & Barki, 2019)**, squaretail grouper **(Karkarey *et al*., 2019)**, short fin molly **(Furness *et al*., 2020)** and swordtails **(Liotta *et al*., 2021)**. In the present study, *M. rosenbergii* showed dominance hierarchies through their behavioral activities and phenotypic expressions. Experimental results showed that at various interactions or ratios males' behavior and characteristics were influenced by male-male and male-female interactions.

It resembles that territory occupation tendency found in those treatments where female was present with male. The result revealed that females' continuous accompany influenced males to develop their aggressive or dominant characteristics. Such characteristics of male were observed to dominate over other male as well to protect their territory, food and breeding sites from other studies. For example, **McGhee *et al*. (2007)** found that males of bluefin killifish (*Lucania goodie*) were territorial, dominant and had tendency to retain their territories, where females circulated among dominant male territories naturally and these males also uphold the tendency to maintain their territory through female. Another study with three-spot damsel fish (*Eupomacentrus planifrons*) showed that males not only recognized different species, but also possessed their territories from other species **(Myrberg & Thresher, 1974)**. **Reebs (2008)** confirmed that single individuals or breeding pairs formed territory for defending their resources or other factors (e.g. food, shelter, a sexual partner, spawning sites or offspring) in many fishes. **Hixon (1981)** found that large male of California reef fish (*Embiotoca jacksoni*) dominated on other males and formed territory in reef caves for mating during breeding.

The present study showed that females had perceptual systems which helped them to choose those males not accompanied with females. The study also revealed that male-male interactions could help to preserve their energy to decorate themselves for female choice. Moreover, female desired those males which had larger chelate leg and persisted without female. The findings of **McGhee *et al*. (2007)** on blue fin killifish (*Lucania goodeiase*) revealed that males were preferred by the female which were not appeared dominant as well as not spawned. Another finding of **Snedden (1990)** on crayfish (*Orconectes rusticus*) revealed that female avoided mating attempts from small-clawed males than from large-clawed males. These fondness of female centered on the phenotypic presences of male.

The current results revealed that male-female interactions influenced to develop total length than male-male interactions. According to the present study, males that were continuously with females were territorial and larger, while non-territorial males were devoid of female and shorter. The present study was supported by the finding of **Korzan *et al*. (2008)** on cichlid (*A. burtoni*) who confirmed that female continuous company influenced males to attain more length and weight than the non-territorial males which remained shrank or same in length. Contradicting this finding, **Hofmann *et al*. (1999)** reported that non-territorial male of cichlid (*Astatotilapia burtoni*) grew faster than the territorial males in both stable and fluctuating environments.

In the study, it was also found that T_2 (1M : 5F) attained significantly more blue color than T_1 (1M) ($P<0.05$). This indicates male-female interactions facilitated to attain different color pattern and develop various morphotypes of male. It also revealed that female's continuous company influenced males to attain significantly more blue color, aggressive behavior and territory formation. Similar observation was detected in the study of **Korzan *et***

***al*. (2008)** showing that territorial males possessed more bright blue or yellow body colors, while non-territorial males were pale in color in cichlid (*A. burtoni*). Introduction of color pattern was also influenced by male-male competition in the genus *Pundamilia* **(Dijkstra *et al*., 2005)**. **Kodric-Brown (1996)** worked on pupfish (*Cyprinodon pecosensis*) showing that when only males were present, breeding coloration was poorly developed, but the coloration was more with the presence of female. In male of *A. burtoni*, the changes in breeding color patterns occurred by the levels of circulating androgens, and these levels changed as a result of agonistic interactions with conspecifics and also with sexual interactions with females **(Fernald, 1976)**.

This present study specified that there were more competition among the males which influenced molting and attained bigger 2^{nd} chelate leg than the mixed culture with females. **Sarkar *et al*. (2012)** showed that larger males of *M. roserbergii* were dominant which had largest carpace, and longer and red colored 2^{nd} chelate leg. Similar findings were reported in the study of **Claverie and Smith (2010)** on squat lobster (*Munida rugosa*) where male displayed a series of distinction in chela (claw) and some individuals attained alrched chela that arose through male–male competition. Another finding of **Dinakaran and Soundarapandian (2009)** on three spot crab (*Portunus sanguinolentus*) revealed that larger male contained bigger chelate leg than small male in a population.

CONCLUSION

The results of this study complement those of field research that illustrate different factors influenceing the behavioral and phenotypic traits of *M. rosenbergii* males at various levels of interactions among male-male and male-female. Male-female interactions showed the territory occupation tendency and developing aggressive or dominant characteristics of male, which finally influence to develop larger total length and cause the emergence of blue and/or orange chelate legs in male, and these males are economically profitable and reproductively effective than other males and females. Male-male interactions also showed longer 2^{nd} chelate leg length. This study also shows the roles of intra-sexual and inter-sexual effects on the expression of phenotypic traits in this species. These attributes are thought to be the indicators of development of important or fruitful characteristics of male prawn and hence to confer benefits to the reproductive success. The present study would provide baseline information on behavioral and phenotypic traits of male prawn. More experiments are needed to explore the interactions within and between sexes in order to better understand the relationship between adaptation, aggression and sexual preference in this species.

Ethical Statement

All animal experiments were conducted in accordance with the approval of Animal Ethics Committee at Khulna University (Research ref. no.: KUAEC-2017/05/12).

Author Contribution

Yousef Ahmed Alkhamis: Conceptualization, data curation, formal analysis, writing-original draft, methodology, fund acquisation; Tania Sultana Mohona: Writing review and editing, formal analysis, data curation, and validation; Roshmon Thomas Mathew: Writing-review and editing, project administration, investigation and validation ; Md. Ayaz Hasan Chisty: Investigation, formal Analysis, data curation; Md Moshiur Rahman: Conceptualization, formal analysis, methodology, investigation and validation, writing-original draft, review and editing, supervision; Ganesan Nagarajan: The resources, data curation, investigation and validation, writing-review and editing; Tushar Mahmud: Formal analysis, the writing-review and editing; Rashid Saleh Alngada: Writing-review and editing, resources, formal analysis; Raed Abdulwahed Alabdulwahed: Writing-review and editing, data curation, nvestigation; Sheikh Mustafizur Rahman: Writing-orininal draft, review and editing, supervision; conceptualization, methodology, project administration, supervision, All of the authors read and approved the final manuscript.

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