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ORIGINAL ARTICLE

Pitchaimuthu Mariappan · Chellam Balasundaram

Sheltering behaviour of *Macrobrachium nobilii* (Henderson and Matthai, 1910)

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Abstract Shelter acquisition seems to be one of the main causes for agonistic interactions in the communal culturing of decapod crustaceans, leading to reduction in survival and growth-rate values. Understanding how to reduce aggressive behaviour among individuals by providing suitable shelters would promote production efficiency and welfare in such aquaculture environments. Factors influencing the sheltering behaviour of a freshwater prawn, *Macrobrachium nobilii*, were studied in laboratory conditions. Prior ownership significantly increased the ability to retain a shelter; males were significantly more likely to acquire and retain a shelter than females, except females carrying eggs. Various movements of the prawn while acquiring the shelter and the behaviour pattern involved in evicting an occupant are described. The size of the shelter selected by an animal is directly related to its body size. Regarding the choice of the colour of the shelter, juveniles and adults preferred dark shelters over light-coloured shelters and never chose a transparent shelter.

Keywords Chelae · *Macrobrachium nobilii* · Prior residence · Shelter selection

Introduction

The recent AQUA 2000 conference at Nice, France brought together behavioural biologists working on ways to improve production efficiency, promote the welfare of the animals, and minimise adverse effects on the environment in the interest of responsible aquaculture. A thorough understanding of feeding, anti-predator, and competitive behaviour can help to domesticate wild populations for farming. To this end, the study of the behaviour of freshwater prawns *Macrobrachium* spp. in a social environment will pave the way to reducing the frequency of interactions between conspecifics. In the communal culturing of decapod crustaceans aggressive and agonistic behaviour generally lead to reductions in survival and growth rate (Aiken and Waddy 1988). The aggressive and agonistic behaviour of crabs *Callinectes sapidus* (Huntingford et al. 1995) and lobsters such as *Homarus americanus* (Atema and Cobb 1980) has drawn more attention than that of other decapods. A few studies are also available on freshwater prawns such as *M. rosenbergii* (Barki et al. 1991a, 1991b) and *M. australiense* (Lee and Fielder 1983).

In the communal culturing of decapod crustaceans (i.e. *Procambarus clarkii*, *H. americanus*, and *M. rosenbergii*) provision of suitable and adequate shelters as substrates for subordinate individuals can minimize adverse interactions (Figiel and Miller 1995; Tidwell et al. 1999). In their natural environment these crustaceans live under crevices, burrows, and pebbles or inhabit empty gastropod shells (Stein 1977) that offer protection to the individuals from adverse inter- and intra-specific encounters (Garvey and Stein 1993). The strategies adopted to minimize encounters vary among different crustaceans. For instance, after a meal, the shrimp *Crangon* spp. digs into the soft sand bottom to hide temporarily. When threatened, the brachygnathous crab *Grapsus grapsus* (Crane 1947) and shore crab *Pachygrapsus crassipes* (Hiatt 1948) hide under rocks. Adult lobsters *H. americanus* make burrows of suitable size under rocks by removing stones and gravel; on sandy bottoms they burrow under stone (Havinga 1929).

Selection of a suitable shelter is an important criterion for survival of these decapods. Juveniles of *Helice tridens* and *Hemigrapsus penicillatu*s evade cannibalism by selecting appropriate shelters that suit their body size (Kurihara et al. 1989). Adult *Orconectes rusticus* more often select dark shelters or covered places than trans-

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P. Mariappan (✉) · C. Balasundaram
Crustacean Aquaculture and Behaviour Unit (CRABU),
Department of Animal Science,
Bharathidasan University, Tiruchirapalli, 620024, India
e-mail: mnobilii@rediffmail.com
Tel.: +91-431-2407040
Fax: +91-431-2407045

parent shelters, but juveniles prefer an open area (Steele et al. 1997).

Obtaining and retaining a given shelter involves aggressive interactions between competing individuals. The ability to hold and retain a given shelter depends upon various abiotic and biotic factors such as the size and shape of the shelter and the sex of the animals. A dominant animal (usually a larger animal) is able to acquire a shelter more readily than subordinate ones (Edsman and Jonsson 1996; Pavey and Fielder 1996). If the size difference between the competing animals is small, a prolonged fight ensues to determine the ownership (Peeke et al. 1995; Huntingford et al. 1995). Normally males win the fight over females (Figler et al. 1995a, 1995b), but when a female is berried there is a corresponding increase in motivation to fight for a long time to win a given shelter (Leimar and Enquist 1984). In crayfish, *Pacifastacus leniusculus*, the berried females always win against males or non-berried females (Peeke et al. 1995). Such maternal aggression for shelter is a necessity to safeguard the brood. Prior residence is another important criterion that enables the resident to retain its shelter in a contest (Ranta and Lindström 1993; Peeke et al. 1995; Blank and Figler 1996; Edsman and Jonsson 1996). For example, in the lobster *Homarus americanus* (O'Neill and Cobb 1979) prior residence is an important factor in determining the outcome of a contest but in the shrimp *Palaemon elegans* it is less important (Evans and Shehadi-Moacdieh 1988).

For the present study, the freshwater prawn, *M. nobilii*, which is endemic to the Cauvery River, south India, was used as the experimental animal. In vernacular *M. nobilii* is called *Kal Rattu* (stone prawn) because of its affinity for boulders and shelters. The culturing of *M. nobilii* is encouraged because of its commercial value, the simplicity with which it is cultured, and its contribution to rural nutrition (Sindhukumari and Pandian 1987). *M. nobilii* is found abundantly along the entire stretch of the Cauvery River and also in south-east India, New Caledonia, Gavataks, and Tuamotu Island (Holthuis 1950). It is a diecdysic prawn, moulting and breeding once in 19±2 days (Balasundaram 1980). Female *M. nobilii* attain sexual maturity at 34 mm (total length; total weight: 0.450 g) and grow to a maximum size of 71 mm (7.2 g). The maximum size of the male is 77 mm with 13 g total weight (Mariappan 2000). *M. nobilii* are characterised by their prominent second pair of chelate legs where one chela differs from the other in form and function (Mariappan and Balasundaram 1997). Like other species of the genus *Macrobrachium, M. nobilii* are more aggressive and in a given population 16.41% of the individuals incur one or more limb autotomy (Mariappan and Balasundaram 1999a), which is a survival strategy found in most decapod crustaceans to evade predation and cannibalism during inter- and intra-species competition for limited resources (Juanes and Smith 1995). Partial exuviation and limb autotomy were also reported even in an ideally reared laboratory population of male *M. nobilii* (Mariappan and Balasundaram 1999b). It is evident that provision of suitable shelters in communal culture environments of *M. nobilii* minimises limb autotomy, thus enhancing survival and growth (Mariappan and Balasundaram 2004).

Our objective with this study was to clarify how some of the already described factors influence shelter acquisition and maintenance in the freshwater prawn *M. nobilii*. We specifically looked at prior residence, ontogenic stage, moult stage, loss of chelae, laterality of chela, and sex of the individual. In the case of females we distinguished between berried and non-berried females to show maternal aggression. We also looked for possible preferences for specific shelter characteristics such as size and colour (opaque dark shelter, opaque white shelter, transparent shelter, or open area).

Methods

Experimental animals *Macrobrachium nobilii* (Henderson and Matthai 1910) were collected from the Cauvery River, near Tiruchirapalli (10.50°N, 78.43°E), and stocked in large cement holding tanks for different experiments. All the experiments were conducted in cement aquaria (100×60×60 cm) under normal laboratory conditions (12:12 D:L; 28±2°C) with minimal disturbance. The bottoms of the aquaria were strewn to a depth of 2 cm with an evenly spread layer of fine sand collected from the river.

Dyadic contests for shelters

The experimental aquarium was partitioned by a removable opaque partition placed in the center. Experiments were conducted separately with ten replicates for each treatment. The studied treatments were prior residence (or prior ownership) in a shelter, sex, maternal stage (berried and non-berried), presence of chela, and laterality of the chela (right-side-dominant vs left-side-dominant animal; also see Mariappan and Balasundaram 1997). In prior-resident experiments 'the resident' prawn was allowed to occupy the shelter for a period of 24 h before the introduction of a non-resident prawn. In non-resident contests both prawns were introduced simultaneously into the experimental aquarium but interaction between the two was prevented by the partition. After an acclimation period of 10 min the partition was removed and an inverted V-shaped country tile (22 cm in length) was placed in the center of the aquarium as shelter. One end of the shelter was blocked with nylon net to ensure exit/entry through the same end. Shelter occupancy was recorded 24 h after the introduction of the second prawn. The pair member in possession of the given shelter was the winner of the contest, as in previous studies with decapod crustaceans (Ranta and Lindström 1993; Blank and Figler 1996). Each animal was used only once; after each experiment the aquarium was thoroughly cleaned and the water was changed to eliminate pheromonal contamination (Caldwell 1985). To identify the factors influencing the outcome of the experiments, each treatment was considered as a single factor. Care was taken when pairing the animals to avoid size differences in the same category. In the autotomy treatment, animals collected in the field that had incurred loss of one limb (major chela of second pair of pereiopod), were used. For moult stage, animals were kept individually in plastic aquaria and moult history was maintained. Freshly moulted animals were used after a minimum period of 12 h from the ecdysis.

Since the outcome of the experiments was our focus, the descriptions of the behavioural acts of the animals are provided rather than the quantification of the behavioural acts. Data on the ability to hold and retain the shelter were tested through chi-square.

Table 1 Outcome of shelter competition between a pair of *Macrobrachium nobilii*. *NR* non-resident; *present* major chela intact; *absent* major chela autotomised; *right* right-side dominant animal; *left* left-side-dominant animal

Treatment		Outcome of prawn A			Chi-square value	Significance
Prawn A	Prawn B	Win	Lose	Share		
Resident	Resident	10	20	70	6.21	*
Resident	Non-resident	80	20	–	10.5	**
Male resident	Female[a] resident	60	–	40	5.64	*
Male resident	Berried resident	10	70	20	6.21	*
Female[a] resident	Berried resident	–	70	30	7.46	**
Juvenile resident	Juvenile resident	70	–	30	7.46	**
Intermoult NR	Freshly moulted NR	100	–	–	13.6	***
Major chela						
Present NR	Absent NR	80	–	20	10.5	**
Absent NR	Present NR	30	–	70	7.46	**
Absent NR	Absent NR	70	–	30	7.46	**
Right NR	Left NR	80	–	20	10.5	**
Left NR	Right NR	10	70	20	6.21	*
Left NR	Left NR	70	–	30	7.46	***

* $P<0.05$; ** $P<0.01$; *** $P<0.001$
[a] Non-berried

Shelter-size preference

The relationship between the size of the shelter and the size of the animal was studied. Three polyvinyl chloride (PVC) pipes with respective diameters of 16, 22, and 30 mm were randomly placed in the experimental aquarium filled with freshwater to a depth of 50 cm. Three prawns of different size (cephalothorax length 10±2, 15±3, and 24±2 mm) were introduced into the center of the aquarium. Each prawn had free access to occupy different-sized shelter since a single shelter open at both ends can accommodate more than one prawn. After 24 h the aperture size of the shelter and the size of the occupying animal were recorded. The observation was repeated ten times with fresh animals. The relationship between aperture size and the cephalothorax length of the occupying prawn was quantified through Pearson correlation coefficient.

Shelter-colour preference

In this experiment, the relative importance of darkness of the shelter was studied using black, white, and colourless (transparent) shelters. Juveniles and adults of *M. nobilii* (ten animals/experimental set per treatment) were selected randomly from the stock tanks and introduced individually into 25-l plastic aquaria. After a lapse of 24 h, the location of the experimental animals was recorded. Previously used animals were not used in this experiment since prior experience may alter the behaviour of the animal. In the first experiment the choice between black shelter and open area was studied by introducing a black PVC pipe shelter into each experimental arena (10×2 cm). In the next experiment white PVC pipes (reduced darkness) were provided instead of black PVC pipe and the shelter occupancy was observed. A clear transparent glass tube was placed in the third experimental aquaria to study the preference for transparent shelters. For the final set of experiments, black and white PVC pipes were placed together in the experimental aquarium to study the preference for these two shelters. Since neither juveniles nor adults occupied the transparent shelter the subsequent treatments for transparent shelter were not provided. Experiments were repeated three times with fresh animals and the data on shelter preference were compared using Student's *t*-test after arcsine transformation of the data.

Results

Dyadic contests for shelters

Data obtained on sheltering behaviour for the chosen treatments are given in Table 1. All the tested factors (i.e. prior residence, sex, moult stage, presence or absence of chela, and laterality) played a significant ($P<0.05$) role in the sheltering behaviour of *Macrobrachium nobilii.* A pair of autotomised animals shared the shelter readily. In acquiring and retaining a given shelter, possession of chela is an added advantage ($P<0.05$; Table 1). When a contest arises between a male and female, normally the male wins since it is larger in size and more dominant than the female. However, in 70% of contests between a male and a berried female and between a non-berried female and a berried female, the berried female won the shelter against its opponent (Table 1). Intermoult *M. nobilii* were more dominant than the freshly moulted prawns.

Shelter-size preference

There is a direct relationship between the animal size and the aperture size of the shelter ($Y=-2.34+0.856X$, $n=30$, $r=0.877$; $P<0.01$). A small animal (10±2 mm) always occupied a small shelter (diameter=16 mm) and larger animals above 22 mm selected large shelters (30 mm diameter). Moreover, the small *M. nobilii* never occupied the large shelter. However, medium-sized prawns occupied any shelter regardless of size.

Shelter-colour preference

In the first experiment, among juveniles and adults 73.33% and 86.60%, respectively, were found occupying shelters and the rest in the open area, which differed significantly among the juveniles ($df=2$; $t=9.91$; $P<0.05$) and adults ($df=2$; $t=15.57$; $P<0.05$), indicating a clear

Table 2 Percentage (mean±SE) of juveniles and adults occupying different types of shelters. A dash (–) indicates an option that was not available in the particular experiment, and 00 indicates 0% occupancy for the available option

Experiment	Stage	Shelter type			
		Black	White	Transparent	Open area
1	Juveniles	73.33±3.34	–	–	26.66±3.34
	Adults	86.66±3.34	–	–	13.33±3.34
2	Juveniles	–	100	–	00
	Adults	–	100	–	00
3	Juveniles	–	–	00	100
	Adults	–	–	00	100
4	Juveniles	76.66±15.19	23.33±15.19	–	00
	Adults	66.66±6.68	33.33±6.68	–	00

preference for black shelters. The percent occupancy of shelter between juvenile and adult *M. nobilii* did not vary ($P>0.05$, $t=3.53$, $t_{0.05}=4.303$, $df=2$). In the second experiment, in which white PVC pipes were provided, all the juvenile and adult *M. nobilii* were found in shelters. When transparent shelters were offered in the third experiment all the juveniles and adults were found in the open area (Table 2). In the last experiment, in which both black and white PVC pipes were placed together to find out the preference between the two, 86.66% of the juveniles and 66.66% of the adults were observed in black PVC shelters and the rest were found in white PVC shelters (Table 2). Though there is a difference in the shelter-colour preference, the pattern of preference between juveniles and adults does not vary significantly ($P>0.05$).

Discussion

Observations made in the laboratory on shelter competition indicate that *Macrobrachium nobilii* is aggressive and readily enters into an encounter with either a resident or a non-resident. *M. nobilii* always enters a shelter first by its anterior region; while doing so the antennae flick (antennules whipping; Lee and Fielder 1983) frequently to check for the presence of any occupant. If the shelter is vacant, the prawn enters into the shelter in the posterior direction with its uropod first. After occupation it comes out within 5±2 min and scans the entire aquaria by walking and/or swimming once or twice around. Then it returns to the shelter again. *M. nobilii* is nocturnal and usually hides in the shelter during daytime with its entire body withdrawn into the shelter. At dawn and dusk it comes out with its head partially protruding outside the shelter with antennule flicking. Sometimes the animal holds the chelipeds in the meral spread position, blocking the entrance of the shelter, then comes out from the shelter and walks around gathering food with a fully stretched abdomen. Then the pereiopods are partially lifted off the substratum and positioned at about 90°, done by bending carpus and merus. In this posture, the prawn gently walks in the anterior direction.

While probing a shelter, if there is an occupant, the intruder, with its chelipeds poked into the shelter (cheliped extension; Barki et al. 1991a), attempts to enter the shelter. Immediately the resident animal responds by pushing the intruder away with the help of its chelipeds (cheliped scissoring and body push; Lee and Fielder 1983); subsequently it comes out to chase the animal away from its territory. If the resident is a larger prawn it effectively prevents the entry of the intruder by blocking the entrance in the meral spread position. Normally the resident animal raises its cheliped towards the opponent. If the intruder also starts displaying its chelipeds a tug of war between the two individuals ensues until the ownership of the shelter is established. If the intruder is less dominant it fails to evict the occupant. In such cases the intruder moves off and turns from the shelter using backwards propulsion by abdominal flexion. This type of backing off is a type of submissive behaviour reported in submissive animals in *Homarus americanus* by Scrivener (1971) and O'Neill and Cobb (1979). If the intruder evicts the resident, the evicted prawn makes an attempt to restore its ownership. Schafer (1954) observed the claw raised above the substrate position while backwards swimming as defensive behaviour in *Carcinus* and *Macropipus*. While probing an occupied shelter, *Panulirus interruptus* and *Palaemon* spp. stretch out chelipeds towards the opponent to threaten. While fighting with the occupant, the intruder keeps its abdomen extended so as to back off readily (cf. Schone 1961).

Among crustaceans, to establish a dominance hierarchy the chelae are used as weapons during aggressive and agonistic displays through visual and tactile signals (Barki et al. 1992, 1997). In this study, competition for a given shelter indicates that the presence of chelae is an added advantage over a conspecific animal without chelae. When competition arose between a pair of autotomised animals, in 30% of the contests individuals without chelae readily shared the shelter. Similarly when one of the pair was autotomised, the handicapped prawn became submissive and co-occupied with the dominant animal (Table 1), since removal of a chela eliminates all stimulus components associated with the chela (Conover and Miller 1978). In *Alpheus heterochaelis* (Conover and Miller 1978) and *H. americanus* (O'Neill and Cobb 1979) also the autotomised and dactylus-immobilised animals could not compete with normal individuals for a given shelter. Further, the larger chela of *A. normani* produces a loud sound that is used as a signal to dominate others

(Nolan and Salmon 1970). Further, the laterality also equally affects the outcome of a shelter competition.

Though in *M. nobilii* prior residence is an added advantage in retaining a shelter, a mixed outcome has been reported for other crustaceans (O'Neil and Cobb 1979; Peeke et al. 1995; Figler et al. 1999). The advantage of prior residence was first described by Braddock (1949) and has been discussed within a territorial context in fishes by Figler et al. (1976) and also in marine crustaceans (Peeke et al. 1995). In crayfish, *Procambarus clarkii* a 24-h prior residence did not influence the outcome of the shelter competition (Figler et al. 1999). As for female *Palaemon elegans*, prior occupancy of a given shelter is of less importance since they usually keep moving from place to place (Evans and Shehadi-Moacdieh 1998). But in male *H. americanus* (Atema and Cobb 1980) and female *Pacifastacus leniusculus* (Doroshenko 1987) prior residence plays a significant role in their reproductively active period. Normally sex differences play an important role in the outcome of aggressive interactions. In general males are dominant over females (Ameyaw-Akumfi 1976; Figler et al. 1995a, 1995b), but 'a reproductive status advantage' is found in *P. leniusculus* and *Procambarus clarkii*, where berried females are more aggressive (Peeke et al. 1995; Figler et al. 1997) than non-berried females and males since they need shelters to incubate and safeguard their eggs. They fight intensively to establish dominance hierarchy over non-maternal females and even adult males (Leimar and Enquist 1984; Ranta and Lindström 1993). Such an aggressive behaviour is also found in *M. nobilii* in this study; in a field population, as well, increased encounters for shelters lead to more limb loss among maternal females (Mariappan and Balasundaram 1999a). Shelter sharing with non-berried females by males is not because of the possibility to mate, since there are different types of adult females (Llloyd and Yonge 1947; Chittleborough 1976; Sandifer and Smith 1979). In year-round breeders like *M. nobilii* four types of females, namely, neuter females with dormant ovaries, neuter females with developing ovaries, incubating females with dormant ovaries, and incubating female with developing ovaries, are found (Pandian and Balasundaram 1982; Balamurugan et al. 2002). In *M. nobilii* the intermolt individuals are more dominant ($P<0.05$) than the freshly moulted ones; such freshly moulted animals are less dominant in aggressive interactions until the exoskeleton hardens (see Schone 1961).

The positive relationship between body size and shelter aperture indicates that size-matched shelters are preferred since they offer more protection during encounters. Small grapsid crabs, *Hemigrapsus penicillatus* evade cannibalism when they settle down in narrow gaps between boulders and stones, which ensures population stability (Kurihara and Okamoto 1987). The salt marsh mud-crab, *Helice tridens* secures protection from larger competitors by hiding in size-related burrows. Since the shelter size plays a major role in survival, in a heterogeneous population, provision of different types/sizes of shelters helps to accommodate animals of different sizes (Aiken and Waddy 1988; Nyström 1994). Like size of shelter, darkness of the shelter also plays a major role in shelter selection by *M. nobilii*. Such an influence of darkness in shelter selection of crayfishes like *P. clarkii* and *Orconectes rusticus* are reported in earlier studies (Alberstadt et al. 1995; Antonelli et al. 1999).

Heterogeneous growth of *Macrobrachium* leads to hierarchy, aggravating cannibalism and territorial behaviour (Karplus et al. 1989). In *M. rosenbergii* three morphotypes result due to much growth. Indeed even individuals of the same brood exhibit mixed growth pattern. Therefore provision of different sizes of shelters that are of black colour not only can minimise limb loss but can also circumvent negative impacts such as aggression and cannibalism.

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