AGONISTIC BEHAVIOR OF THE FRESHWATER PRAWN *MACROBRACHIUM LAR* IN RELATION TO SIZE AND SEX

by

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Stephen G. Nelson, Chairman, Thesis Committee

The agonistic behavior of the freshwater prawn *Macrobrachium lar* was measured to determine whether or not differences in size, weight, and sex between opponents influenced its expression. Data were collected during 10-minute dyadic encounters of male-male, male-female, and female-female pairings. Individual aggressive and submissive acts were described and their frequencies of occurrence recorded. An agonistic index, consisting of the total number of aggressive acts committed per individual per match divided by the total number of aggressive and submissive acts per individual per match, was calculated for individuals of each match as a measure of agonistic behavior. Other measures of agonistic behavior were recorded, including the number of bouts per match, the fighting response latency per match, and the accumulated attack time per match. Additionally, records of matches won by large opponents in dyadic encounters were recorded.

No significant correlations of differences in either the carapace length or weight with agonistic index, the number of bouts per match, the fighting response latency or the accumulated attack time could be determined. The relations between the accumulated attack time and weight and the fighting response latency and the number of bouts per match were correlated for male-male and female-female pairings respectively. A significant difference was found between male-male, male-female, and female-female matches in the mean values of the agonistic index. No significant difference could be determined for mean values of the number of bouts per match, the fighting response latency, or the accumulated attack time. Individual aggressive and submissive acts were quite variable within groups. Larger animals did not have significant advantage in winning success in intrasexual encounters but they did in intersexual encounters. Differences in the agonistic index were found between winners and losers, winners having a high mean agonistic index value with little variation while losers had a low mean agonistic index value with considerable variation.

TO THE GRADUATE SCHOOL AND RESEARCH

The members of the Committee approve the thesis of Terry John Donaldson presented 3 August 1981.

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INTRODUCTION

Agonistic behavior is that which conveys both aggression and submission. It consists of acts of attack, escape, threat, defense, and appeasement (Scott and Fredericson, 1951). These acts are related physiologically and usually occur together both temporally and spatially (Brown, 1975).

A number of factors have been shown to affect the level of agonism expressed by crustaceans. Two commonly measured influences on agonism are the effects of size and sex differences. In crayfish, such as the genera Cambellus, Procambarus, and Orconectes, large individuals are dominant in intraspecific encounters (Bovbjerg, 1956; Lowe, 1956) or at least possess an advantage over them in combination with other factors (Rubenstein and Hazlett, 1974). Larger spiny lobsters, Panulirus interruptus, exhibit a higher proportion of aggressive behavior than do smaller animals (Roth, 1972). Size (Hazlett, 1966) is also an advantage in males of the hermit crab Calcinus tibicen. Large hermit crabs, Clibanarius vittatus, are more aggressive than small crabs and as the difference in size between the two opponents increases, the probability of each contestant ignoring the other also increases (Hazlett, 1968). Sinclair (1977) reported a similar effect for the stone crab Mennippe mercenaria.

The size difference between opponents also affects the onset and expression of agonistic encounters. Large porcillinid crabs of the genus Petrolisthes have been shown to initiate agonistic encounters more often and are more likely to profit from these encounters by successfully gaining or retaining space (Molenock, 1976). Large stomatopods, Gonodactylus viridis, also initiate more attacks and win more often than smaller opponents (Caldwell and Dingle, 1979). Small G. viridis apparently attempt to bluff larger opponents into misjudging size by employing displays which are greater in intensity than those of larger animals (Caldwell and Dingle, 1979). Hazlett and Bossert (1966) showed significant differences in behavior displays of the hermit crab Clibanarius vittatus with changes in the size differences between opponents.

The sex of the opponents may also influence their success in encounters or the expression of agonistic behavior. Such influence may be exaggerated in sexually dimorphic species. In a number of crustaceans where sexual dimorphism is not obvious, males tend to be more aggressive than and dominant to females. Examples of these include the crayfish Procambarus alleni, the spiny lobster Panulirus interruptus, and the stone crab Menippe mercenaria (Bovbjerg, 1956; Roth, 1972; Sinclair, 1977). Ovigerous females of the crayfish Cambarellus shufeldtii dominate males but lose that ability when they are not bearing eggs (Lowe, 1956). Sexually dimorphic ocypodid crabs display less agonism in intersexual encounters than in intrasexual encounters (Crane, 1967; 1975; Warner, 1970). Crane (1967) reported pronounced differences between sexes in the expression of agonistic behavior resulted from differences in the morphological character used for displays of the fiddler crab Uca rapax.

The quantification of agonistic behavior present in a given situation requires an index of measurement. Several such indices have been suggested. These have included the fighting response latency which is the elapsed time between initial contact and actual fighting (Fredericson, 1949), the number of attacks made by one contestant against another in a given period of time (Catlett, 1961), and the accumulated attack time which is the amount of time spent fighting in a given situation (Catlett, 1961). Experiments with the house mouse, *Mus musculus*, have shown these three indicators of aggression to be correlated (Catlett, 1961). Similar indices have been used for the study of crustaceans in order to quantitively assess the effects of a variety of influences on their behavior.

The purpose of this study was to examine the agonistic behavior of the freshwater prawn *Macrobrachium lar* (Fabricius) with attention to the effect of the relative size and sex of opponents on the expression of this behavior and to evaluate a number of methods of assessing these effects. Attention was also paid to variance within measures of this behavior, since many previous studies have neglected this factor. The species *M. lar* was selected, since it is widely distributed in the Pacific basin (Holthuis, 1950) and has been suggested for aquaculture in some areas (Maciolek, 1972; Ling and Costello, 1976).

MATERIALS AND METHODS

Macrobrachium lar were captured in various streams on Guam, Mariana Islands, by electrofishing and trapping. The prawns were maintained individually in freshwater aquariums provided with gravel substrata. Aeration was provided via airstones supplied by diaphragm pumps. The water in each aquarium was changed twice weekly. Timer-controlled lighting provided a 12-hour light-dark cycle. The aquarium were maintained at room temperature (21° C). Although some variation in water temperature and daily light cycle occurred as a result of local power outages and infrequent mechanical malfunctions, these had no noticable effect on the animals. A varied diet of commercially prepared squid flakes, commercial pig feed, and the freshwater alga *Microspora* sp. was provided daily.

An ethogram was constructed using a modification of an experimental method known as the "Boxing Match" (Scrivener, 1971; Atema and Cobb, in press). For each match, two adult intermolt individuals with no prior contact were placed in a 10-ℓ aquarium, which was divided into two equal-sized compartments by a removable opaque plastic partition. Both compartments were provided with gravel substrata. A one-hour period for acclimation to the tank was allowed each animal prior to the onset of a match. A match commenced with the removal of the partition and typically lasted 10 minutes. Matches were allowed to run more than 10 minutes, if the individuals were engaged in a bout when the time elapsed. Bouts were defined as encounters between opponents during the match. Matches were held during the light phase of the photoperiod at various times between 0700-1900h and were timed to the nearest 0.01 second with an electronic stopwatch. Upon completion of the match, the prawns were returned to their holding tanks. Damaged prawns were replaced with others from a community tank. The match tank was cleaned after each match to minimize possible contamination from pheromones.

Preliminary observations led to the recognition of agonistic acts. The type and frequency of those acts exhibited during each match was recorded by voice on a tape recorder and transcribed for analysis. These acts were classified as either aggressive, submissive, or neutral. Additionally, the number of bouts per match, the fighting response latency, and the accumulated attack time were recorded. Won-loss records were also kept for all matches.

Data were derived from 75 dyadic matches. Twenty-five matches each were run for male-male, male-female, and female-female pairs. A total of 24 males and 15 females were used in the study. Males ranged in size from 21-41mm carapace length and from 8.17-27.51g wet weight. Females ranged in size from 20-31mm in carapace length and from 7.20-17.84g wet weight. A number of individuals of both sexes were used more than once, but at no time were two individuals paired together more than once.

The carapace length (mm) of each prawn was determined by measuring the distance from the posterior margin of the orbit to the posterior edge of the carapace. The weight of each prawn was determined from the length-weight relation described by Weatherly (1972) in accordance with the formula:

$$\text{Log } W = \text{Log } A + n \text{ Log } L$$

where W = wet weight (g), L = carapace length (mm), and both A and n were determined empirically. A correlation coefficient of $r = 0.8543$ ($p < 0.05$) was calculated for the line of best fit for this relation for a sample size of 22 prawns and A and n were determined to be 1.04 and 0.8463 respectively.

The sex of each prawn was determined by inspection of the chelipeds and by calculation of the ratio of the carapace length to the width of the second abdominal segment. It was previously determined that a ratio greater than or equal to 2.0 indicated that the prawn was a male (Stephen G. Nelson, unpublished data).

An agonistic index was calculated to indicate individual levels of agonistic behavior in dyadic encounters. It consisted of the total number of aggressive acts committed by an individual per match divided by both the aggressive and submissive acts committed by this individual. Analysis of the influence of carapace length and weight differences on agonistic behavior was made by calculating correlation coefficients for the relation between these differences and the agonistic index. The number of bouts per match, the fighting response latency, and the accumulated attack time were treated in this manner. Additionally, correlation coefficients were calculated for the relation between the accumulated attack time and the fighting response latency, the accumulated attack time, and the number of bouts per match, and the fighting response latency and the number of bouts per match.

Analysis of variance was used to determine whether the sex of the opponents affected the agonistic index, the number of bouts per match, the fighting response latency, and the accumulated attack time. Chi-square tests were used to determine whether large prawns won matches more often in intrasexual encounters.

RESULTS

Individuals of the species *Macrobrachium lar* possess a diverse repertoire of agonistic acts. These include 22 aggressive and 6 submissive acts as described in the Appendix. The frequencies of occurrence of agonistic acts in male-male, male-female, female-female matches are shown in Table 1. Standard deviations in most cases exceeded the mean values.

Table 2 shows the correlation coefficients for the regressions of size and weight differences on the agonistic index in relation to match pairings. These ranged from 0.2894 to - 0.0131 for match winners and 0.0272 to - 0.3243 for match losers, none of which were significant ($p < 0.05$). Similar results were found for other measures of agonistic interaction with respect to size and weight differences and to each other.

No influence of size or weight differences on the number of bouts per match, the fighting response latency, or the accumulated attack time in encounters could be determined. Correlation coefficients for the regression of differences in carapace length or weight on either the number of bouts per match, the fighting response latency, or the accumulated attack time ranged from - 0.4580 to 0.3170. Correlation coefficients for the regression of the accumulated attack time on either the fighting response latency on the number of bouts per match, and the fighting response latency on the number of bouts per match ranged from - 0.4133 to 0.2434 (Table 3). Only two of these values were significant ($p < 0.05$).

Table 1. Mean frequencies (± standard deviation) of occurrence of individual aggressive and submissive acts. Acts were recorded from each 10-minute dyadic encounter (frequencies of occurrence calculated from 50 individuals in 25 matches for each sexual pairing). Acts include: Antennae raise (ANR), Antennae Touch (ANT), Antennule Touch (AT), Antennule Lower (AL), Body Touch (BT), Cheliped Touch (CT), Lie Down (LY), Cheliped Raise (CR), Cheliped Wave (CW), Meral Spread (MS), Scissor (SC), Stand-up (SU), Tail-display (TD), Lateral Display (LD), Approach (A), Chase (C), Lunge (L), NIP (N), Grasp (G), Hold (H), Pin (P), Climb (CB), Lock (LK), Wishbone-posture (WP), Tail-flip (TF), Walk-away (WA), Tail-push (TP), and Abdomen-curl (AC).

Match Pairs	Behavioral Act							
	Aggressive					Submissive		
	ANR	ANT	AT	AL	BT	LD	TD	LY
Male-male	1.30 (1.99)	2.80 (6.43)	0.36 (0.69)	0.12 (0.38)	0.18 (0.48)	0.20 (0.82)	0.10 (0.44)	0.30 (1.02)
Male-female	2.10 (3.08)	1.80 (4.05)	0.02 (0.14)	0.14 (0.85)	0.08 (0.27)	0.00 (0.00)	0.40 (0.28)	0.30 (0.69)
Female-female	0.40 (1.69)	0.30 (0.74)	0.10 (0.72)	0.10 (0.89)	0.50 (1.33)	0.02 (0.14)	0.10 (0.27)	0.40 (0.66)

Match Pairs	MS	CR	CT	CW	WA	TF	AC
Male-male	1.50 (2.71)	0.96 (1.26)	1.60 (2.45)	0.18 (0.43)	1.00 (1.70)	0.60 (1.68)	0.30 (0.48)
Male-female	1.06 (1.53)	1.42 (2.04)	3.06 (5.00)	0.56 (1.16)	1.30 (1.86)	0.90 (1.87)	0.80 (1.35)
Female-female	1.70 (2.22)	1.10 (1.93)	5.90 (10.81)	0.60 (2.12)	1.90 (2.50)	0.60 (1.36)	1.10 (1.74)

Table 1 (Continued).

Match Pairs	Behavioral Acts			
	Aggressive			
	A	CB	SU	SC
Male-male	1.40 (2.05)	0.04 (0.20)	0.26 (1.20)	0.06 (0.31)
Female-female	1.92 (1.89)	0.20 (0.57)	0.34 (0.74)	0.42 (1.44)
Female-female	2.30 (2.50)	0.20 (0.74)	0.40 (3.40)	0.10 (0.31)
	C	L	N	G
Male-male	0.28 (0.67)	0.94 (5.31)	0.32 (1.12)	0.58 (1.47)
Male-female	0.32 (0.68)	0.30 (0.81)	0.68 (1.81)	1.30 (2.91)
Female-female	0.60 (1.17)	0.80 (0.34)	1.00 (2.20)	0.60 (1.44)
	PN	LK	WP	H
Male-male	0.02 (0.14)	0.40 (0.16)	0.10 (0.33)	0.06 (0.31)
Male-female	0.02 (0.14)	0.00 (0.00)	0.00 (0.00)	0.18 (0.52)
Female-female	0.30 (0.33)	0.30 (0.53)	0.30 (0.84)	0.04 (0.20)

Table 2. Correlation coefficients for the relation between difference in either carapace length or weight of opponents and the agonistic index. Correlation coefficients are for winners or losers in both intra- and intersexual *Macrobrachium lar* dyadic matches (sample size given in parentheses).

Difference	r value		
	male-male	male-female	female-female
Size*			
Winner	0.1460 (20)	- 0.0131 (25)	0.1554 (22)
Loser	- 0.0523 (20)	0.0272 (25)	- 0.3243 (22)
Weight**			
Winner	0.1827 (20)	0.2894 (25)	0.1380 (22)
Loser	- 0.4943 (20)	- 0.0955 (25)	- 0.1913 (22)

* Denotes carapace length in mm.

** Denotes wet weight in g.

Table 3. Correlation coefficients of the measures of agonistic behavior in *Macrobrachium lar*. R values indicate the relation between differences in either carapace length or weight of opponents and either the number of bouts per match, the fighting response latency, or the accumulated attack time (value nos. 1-6); the relation between the accumulated attack time and either the number of bouts per match or the fighting response latency (value nos. 7-8); and the relation between the fighting response latency and the number of bouts per match (value no. 9). Sample size for each value is given in parentheses.

Value No.	Relation	r value		
		Male-male	Male-female	Female-female
1	Bouts per Match and Carapace Length*	-0.1973 (40)	0.2584 (50)	0.0100 (44)
2	Bouts per Match and Weight**	-0.1265 (40)	-0.1498 (50)	0.0983 (44)
3	Fighting Response Latency and Carapace Length*	0.1261 (40)	0.0169 (50)	-0.2071 (44)
4	Fighting Response Latency and Weight**	0.3173 (40)	0.2232 (50)	0.0291 (44)
5	Accumulated Attack Time and Carapace Length**	0.0520 (40)	0.1190 (50)	-0.2030 (44)
6	Accumulated Attack Time and Weight**	-0.4582 (40)	-0.0118 (50)	0.2983 (44)
7	Accumulated Attack Time and the Number of Bouts per Match	0.1183 (40)	-0.0252 (50)	0.2434 (44)

Table 3 (Continued).

Value No.	Relation	r value		
		Male-male	Male-female	Female-female
8	Accumulated Attack Time and the Fighting Response Latency	-0.1979 (40)	-0.2352 (50)	-0.2113 (44)
9	Fighting Response Latency and the Number of Bouts per Match	-0.1682 (40)	-0.1554 (50)	-0.4133 (44)

* Denotes carapace length in mm.

** Denotes wet weight in g.

Table 4. Mean values (± standard deviation) of agonistic indices. Values calculated for both winners and losers in Macrobrachium lar dyadic encounters between pairings of the sexes (sample size given in parentheses).

Opponent	Mean Agonistic Index (± standard deviation)*		
	Male-male	Male-female	Female-female
Winner	0.95 ± 0.11	0.93 ± 0.12	0.91 ± 0.16
Loser	0.65 ± 0.28	0.61 ± 0.29	0.48 ± 0.24

* Denotes total aggressive acts per individual per match/total aggressive and submissive acts per individual per match.

Mean agonistic index values for match winners and losers are given in Table 4. Mean agonistic index values for winners from 0.91 to 0.95 with standard deviations of 0.11 to 0.16. Losers had mean agonistic indices ranging from 0.48 to 0.63 with standard deviations of 0.24 to 0.29. Differences in the mean agonistic index between winners and losers were significant (two-way anova, $F = 100.40$, $df = 1$, $p < 0.01$). An example of the difference between winners and losers in agonistic index values is shown in Figure 1. Mean agonistic index values were analyzed for the influence of sex in dyadic encounters. Significant differences (two-way anova, $F = 14.79$, $df = 2$, $p < 0.01$) were found for winners and losers between pairings of the sexes. Interaction between winners and losers and pairings of the sexes was also significant ($F = 166.29$, $df = 2$, $p < 0.01$). Analysis of variation in the measures of agonistic interaction showed considerable variation within groups. The mean number of bouts per match ranged from 2.80 to 4.50 with standard deviations ranging from 68-120% of the mean. The mean fighting response latency ranged from 198.89 to 281.55 seconds with standard deviations ranging from 76 to 93% of the mean. For the mean accumulated attack time, mean values ranged from 102.22 to 117.11 seconds with standard deviations in excess of the mean by 117 to 130% (Table 5). No significant differences for any of these measures could be found between pairings in either intra- or intersexual matches (one-way anova, $p < 0.05$; see Table 5 for individual F values and degrees of freedom for each measure).

Larger males won 9 of 16 and larger females won 7 of 21 intrasexual matches. Larger males won all 24 matches with smaller females; the only match in which a female was larger than a male was won by the

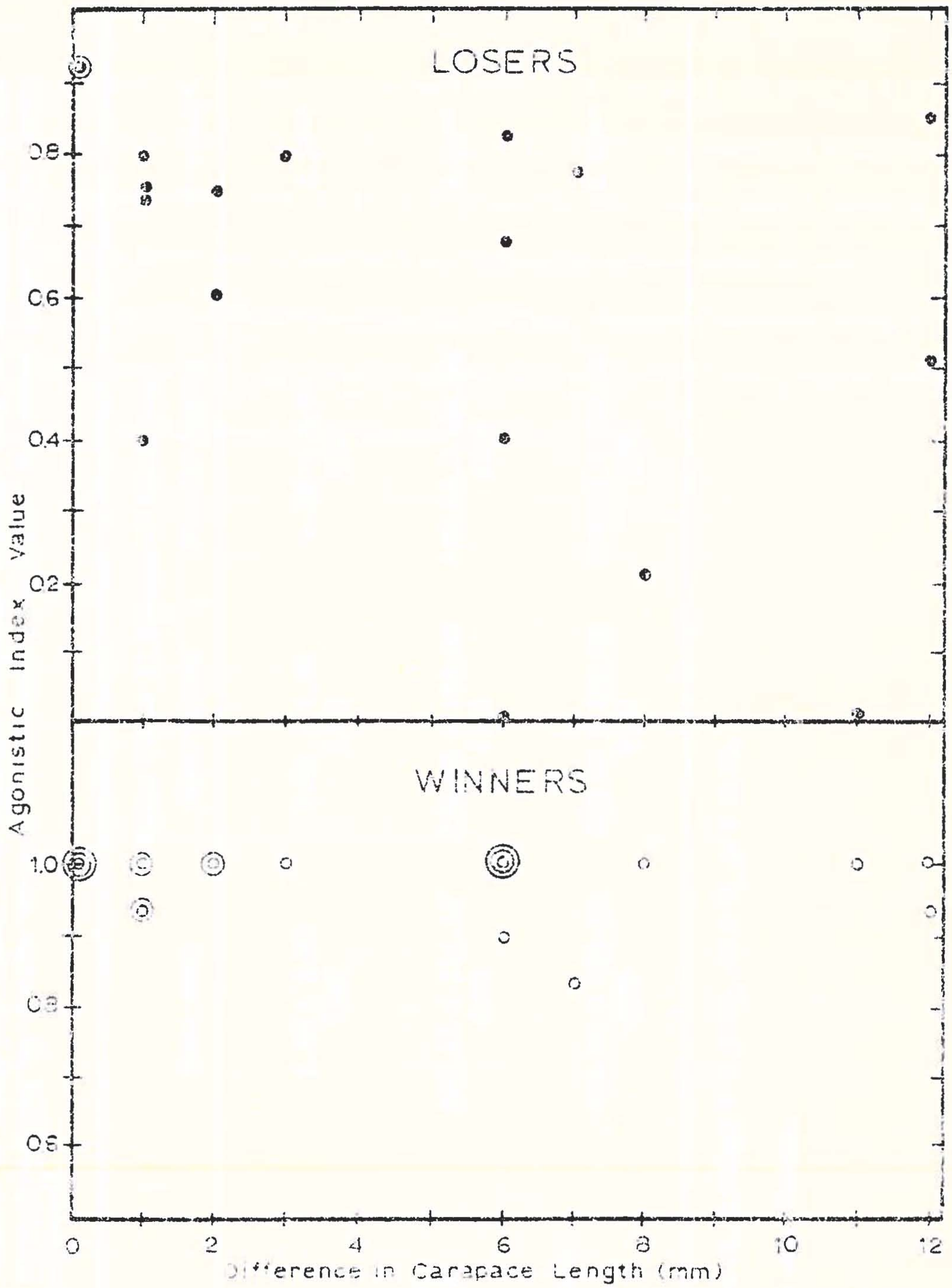

Figure 1. Example of the difference between winners and losers in agonistic index values recorded from dyadic encounters of <u>Macrobrachium lar</u>.

Table 5. Mean values (± standard deviation) of additional measures of agonistic behavior. Values are for the number of bouts per match, the fighting response latency, and the accumulated attack time of Macrobrachium lar dyadic encounters between pairings of the sexes (sample size given in parentheses).

Variable	Mean Value (± Standard Deviation)			
	Male-male	Male-female	Female-female	F value*
Number of Bouts per Match	2.80 ± 3.37 (20)	4.52 ± 3.45 (25)	4.48 ± 3.07 (22)	2.21**
Fighting Response Latency (seconds)	281.55 ± 216.15 (20)	230.56 ± 190.39 (25)	198.89 ± 186.26 (22)	0.94**
Accumulatted Attack Time (seconds)	102.22 ± 133.26 (20)	104.72 ± 122.76 (25)	117.11 ± 147.90 (22)	0.09**

* One-way anova, critical F = 3.07, df = 2, $p < 0.05$.

** Denotes not significant.

female. No significant success of winning was found for the larger animals, either in terms of carapace length ($X^2 = 1.13$, df = 1, $p < 0.05$) or weight ($X^2 = 2.74$, df = 1, $p < 0.05$) for intrasexual encounters. Data were analyzed from 37 of 50 intrasexual matches; drawn matches and matches between individuals without distinguishable carapace length or weight differences were excluded. Matches between inter-sexual pairings were excluded because of the lack of instances in which females were greater in size compared with males.

DISCUSSION

Individual prawns, Macrobrachium lar, are quite active in intraspecific dyadic encounters, and they display high variability of the level of agonism as expressed by a variety of indices. Neither the size nor sex of the opponents had a significant influence on these measures of agonistic behavior. This suggests that M. lar either are not capable of recognizing the size of their opponents relative to themselves or that variation as a result of other factors masks any effect of size.

Size discrimination has been shown to influence agonistic behavior in other crustaceans. The stomatopod Gonodactylus viridis possesses a keen visual sense of size discrimination that influence agonistic interaction by affecting the types of displays made by two opponents (Caldwell and Dingle, 1979). The size of the opponent must be determined by some means in other crustaceans in which this clearly influences success in agonistic encounters. In dyadic encounters, the larger of the two opponents is usually the winner, as has been shown for crayfish (Bovbjerg, 1956; Lowe, 1956), hermit crabs (Hazlett, 1966; 1968), stomatopods (Dingle and Caldwell, 1969; Caldwell and Dingle, 1979), brachyuran crabs (Warner, 1970; Jachowski, 1974; Molenock, 1976; Sinclair, 1977), spiny lobsters (Roth, 1972), and in the Malaysian prawn (Peebles, 1980), Macrobrachium rosenbergii. Reese (1962) reported an exception to this for all small female hermit crabs, Calcinus laeveminus but not for males of the species.

Although larger crustaceans are generally successful in winning encounters, other factors have been found which may influence or mask the effect of size. In studies of Macrobrachium rosenbergii, such variables included molt state of the opponents, the length of time in which they were paired, prior residence, and the presence of shelter (Peebles, 1977; 1978; 1979a; 1979b; 1980). Hazlett (1966) found that in the hermit crab Calcinus tibicen the outcome of the encounter was influenced by sex. In other crustaceans, males and females have been shown to be just as agonistic in intrasexual encounters as in intersexual encounters (Bovbjerg, 1956; Lowe, 1956; Hazlett, 1966; Warner, 1970; Molenock, 1976; Sinclair, 1977; Caldwell and Dingle, 1979).

Male Macrobrachium lar possess a greater body size and proportionally larger chelae than females, and this sexual dimorphism may complicate the separation of the effects of size from those of sex. Sex had a significant effect on the expression of agonistic behavior in M. lar. Additionally, differences in winners and losers in each pairing were noted. Similar agonistic values occurred for winners and losers in both male-male and male-female encounters. In female-female encounters, winners had values similar to those of other pairings but losers had lower values (Table 4). Strong interaction between losing and female-female agonistic expression was indicated, suggesting that females did not fight as much as males in intrasexual encounters.

Another problem relates to the measure of agonism which is chosen. The number of bouts per match, the fighting response latency, and the accumulated attack time were used in measuring fighting between similarily sized house mice, Mus musculus, of the same genetic strain by

Catlett (1961). Accumulated attack time was correlated with the number of attacks (= bouts) per match and the fighting response latency, while the number of attacks was also correlated with the fighting response latency; absolute r values ranged from 0.6387 to 0.9482. In spite of the reduced variation which resulted from the use of genetically and physically similar opponents, some problems with these measures were encountered. Measurement of fighting behavior by the number of attacks presented difficulties because it was hard to decide what actually constituted an attack. Fighting response latency was dependent upon the distance between opponents in a defined area at the onset of the match, since closer opponents could respond faster than opponents separated by a greater distance. Accumulated attack time was favored because it was a continuous rather than a discrete variable and it provided a strong indication of effort spent fighting.

For Macrobrachium lar encounters there was no significant correlation between measures of agonistic interaction (number of bouts per match, fighting response latency, and accumulated attack time) and differences between opponents in carapace length or weight, nor were there significant correlations between any of the measures. Other studies of agonistic behavior in crustaceans have employed a variety of methods. Some determined agonistic levels by won-loss records of opponents. Such measures are useful in determining dominance-subordinance relationships (Bovbjerg, 1956; Lowe, 1956), success in interspecific encounters (Hazlett, 1971) or success in encounters between opponents of different sizes (Hazlett, 1971; Caldwell and Dingle, 1979). Others indicated attack frequencies within bouts or frequencies within matches (Thorp, 1978; Peebles, 1980). Even if studies use similar measures of behavior it may be difficult to compare them if the variation in the indices is not reported or if there are differences in match lengths.

In the present study, the agonistic index, defined as the ratio of aggressive acts to aggressive and submissive acts, provided additional information about the matches. Winners were consistently aggressive and committed few, if any, submissive acts. This was shown by high mean index values of low variation (Table 4). Losers were characterized by lower index values of considerable variation (Table 4). Variation in losers may be explained in part by differences in time until submission occurred. If an individual's mean value was low, it could be because it began to commit submissive acts in response to its opponent's attacks after the onset of the match. If the losing individual's index value was high, it may be because both opponents were aggressive until well into the match when one relented and became submissive. Agonistic encounters could be prolonged, as indicated with the hermit crab Calcinus vittatus and the stone crab Menippe mercenaria, if similarily match opponents maintained comparable levels of agonistic display (Hazlett, 1968; Sinclair, 1977).

Thorp (1978) reported a mean range of 1.10 to 6.50 bouts per period with a standard deviation of the means of 0.40 for one-hour encounters between crayfish Cambarus latimanus. In this study, the mean number of bouts per match for Macrobrachium lar encounters ranged from 2.80 to 4.52 bouts per period with standard deviations of 3.07 to 3.45 (Table 5) for 10 minute encounters. Peebles (1980) reported a range of 1.0 to 3.0 bouts per period in Macrobrachium rosenbergii encounters but did not indicate variation within these values. However, it is also difficult to compare these species directly because the length of a match varies considerably between studies.

Similar difficulties arise in studies of interspecific agonistic behavior. King (1957) measured conflict between the house mouse Mus musculus and the deer mouse Peromyscus maniculatus bairdii through the use of attack frequency, fighting response latency and won-loss records. Mean values with no reported variation were used to quantify the behavior. Studies of interspecific crustacean agonistic behavior are few. Some studies reported a species' winning success in encounters (Reese, 1961; Penn and Fitzpatrick, 1963; Kinzie, 1968; Hazlett, 1971). Hazlett (1971) compared won-loss records from matches between three species of portunid crabs and subjectively categorized agonistic encounters into four groups which ranged from avoidance to hard fighting. Krekorian et al. (1974) compared match initiators as a measure of agonism in encounters between the American lobster, Homarus americanus, the California spiny lobster, Panulirus interuptus, and the rock crab, Cancer antennarius.

Comparison of studies of the agonistic behavior of crustaceans must be made with caution since, as shown in the present study, common measures of agonism may not be correlated even in intraspecific studies. Variability of the indices, if reported, would facilitate such comparisons. In fact, reports of this are so few that it is quite difficult to determine whether or not Macrobrachium lar exhibits exceptionally variable agonistic behavior. If such variability is common, then quantification of agonistic behavior is probably only useful under very specific conditions or with the use of large sample size.

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APPENDIX A

DESCRIPTIONS OF ACTS RECORDED IN THE AGONISTIC BOUTS BETWEEN FRESHWATER PRAWNS, *MACROBRACHIUM LAR*

Appendix A. Descriptions of acts recorded in the agonistic bouts between freshwater prawns, Macrobrachium lar.

AGGRESSIVE

Act	Description
Cheliped Touch	Tapping of the dactyl of the cheliped against an opponent's exoskeleton.
Antennae Raise	Rapid raising and lowering of either one or both antennae.
Antennae Touch	Touching either one or both antennae against the body of an opponent.
Antennule Touch	Touching either one or both antennules against an opponent's body.
Antennule Lower	A rapid lowering of either one or both antennules to the substratum directly in front of the opponent, followed by a slower raising of the antennules.
Body Touch	Placing a part of the body in contact with the opponent's. Often the bodies were positioned parallel to one another.
Cheliped Raise	Elevation of one or both chelipeds above the substratum by as much as 80°. The chelipeds are not parallel to one another.
Meral Spread	Elevation of parallel chelipeds above the substratum.
Cheliped Wave	A rapid cheliped raise followed by a side-to-side motion.
Scissor	Rapid opening and closing of one or both dactyls of the cheliped during a cheliped raise or wave.
Stand-up	Elevation of the body by a complete extension of the ambullatory legs.
Approach	Movement by one animal towards another by walking.

Appendix A (Continued).

Act	Description
Chase	Rapid walking towards a fleeing opponent after a bout, often with chelipeds extended completely forward.
Lunge	A rapid movement towards an opponent, with chelipeds extended and dactyls open.
Grasp	Use of dactyls of the chelipeds in grasping a portion of an opponent's body. Release occurs after a few seconds or holding may ensure.
Hold	Follows grasp; contact is prolonged.
Nip	Rapid closure of the dactyl against the opponent's body. Release follows instantaneously.
Pin	Holding the opponent's body against the substratum with the cheliped.
Lock	Follows a meral spread in encounters. Opponents grasp on another's extended chelipeds and remain in this position, often with rapid body thrusts forward and backward, until one opponent releases the other and flees.
Wishbone-posture	An extension of the lock, in which the opponents raise themselves on their ambullatory legs while still in the locked position. Forward or backward body thrusting occurs very slowly and body shaking also occurs. The posture is terminated when one opponent releases the other and flees.
Climb	Walking over the prone or crouching opponent.
Tail-push	Backing into the opponent using the telson to deflect an opponent's chelipeds.

Appendix A (Continued).

SUBMISSIVE

Act	Description
Abdomen-curl	A curling of the abdomen, often prior to fleeing. The telson is tucked beneath the abdomen.
Lie Down	Lying on the substratum, often with chelipeds folded directly in front of the body.
Lateral Display	A lateral presentation of the extended abdomen to the opponent. The body is elevated just off the substratum.
Tail Display	Presenting the telson to an opponent, usually from a lie-down posture, with the abdomen fully extended.
Walk-away	Moving away from an opponent by walking.
Tail-flip	A rapid flexure of the abdomen with a corresponding release that propels a fleeing animal away from an opponent. Swimming commences after the tail-flip and the flip may be repeated during the course of the escape.