INTRASPECIFIC AGONISTIC INTERACTIONS OF SQUILLA EMPUSA (CRUSTACEA: STOMATOPODA)

by

JENNIFER L. WORTHAM-NEAL [1,2)]
(University of Louisiana at Lafayette, Louisiana, USA)

(Acc. 30-XI-2001)

Summary

Mantis shrimp are benthic, predatory marine crustaceans that have complex agonistic interactions. These crustaceans are divided into two functional groups based on the morphology and use of their raptorial appendage: smashers and spearers. Most research on the agonistic behaviours of mantis shrimp has focused on smasher species and on contests between asymmetrical and same-sex individuals. No studies have investigated the intersexual and intrasexual interactions of size-matched spearer individuals. I conducted a laboratory experiment using *Squilla empusa*, a spearer that lives in the Gulf of Mexico, to determine if agonistic differences exist between males and females. The results suggest that (1) although threat displays are rare in both males and females, male aggressive interactions involving physical contact are common, (2) males engage in more aggressive behaviours and interactions than do females, (3) females are less aggressive toward both males and females than males are toward males and females; interactions involving females are usually passive, non-striking, whereas interactions involving males can result equally in a strike or passive behaviour, (4) males are more aggressive than females, and (5) an increase in the number of treatment individuals resulted in an increase in the number of interactions. The behaviours of *Squilla empusa* are compared with literature reports concerning other species of mantis shrimp. The differences in habitat, feeding method, vision, and burrow type may explain the differences between smashers and spearer agonistic behaviours.

[1)] Present address: University of Evansville, Department of Biology, 1800 Lincoln Ave, Evansville, Indiana 47722, USA; e-mail address: jw232@evansville.edu

[2)] I thank Dick Waller of the Gulf Coast Research Laboratory for access to and help during collecting cruises. J. Akin provided help with experimental design. I thank R. Bauer, E. Loos, and R. Jaeger for critically reading previous drafts of the manuscript. This research was supported by The University of Louisiana at Lafayette Department of Biology and the Graduate Student Organization, the Lerner-Grey Marine Fund for Marine Research from the American Museum of Natural History, and The Louisiana Universities Marine Consortium Foundation, Inc.

Introduction

Intraspecific contests among individuals are usually for a limited resource, such as food, space, or mates. Energy used for agonistic behaviours is not available for feeding and reproduction, and different acts and displays have different energetic costs and risks (Maynard Smith, 1982; Smith & Taylor, 1993). One important function of agonistic interactions is opponent assessment. Escalated contests occur if individuals cannot assess their opponent in terms of size asymmetries or fighting ability (Parker, 1974; Maynard Smith & Parker, 1976; Stamps & Krishnan, 1997). If there is a small difference between contestants, assessment and differences in fighting ability may not be evident initially, and, fights tend to escalate and last longer (Parker, 1974; Mesterton-Gibbons & Adams, 1998). Most aggressive contests are settled without escalation in many taxa because of the cost involved in fighting (Pool, 1995; Stamps & Krishnan, 1997). If one individual is larger or stronger, the outcome of a contest is predictable so there is a benefit to both individuals to settle the dispute quickly.

In crustaceans, assessment ability, levels of aggression and degree of territoriality are often related to habitat type and the availability of resources. The energetic cost of agonistic behaviours may influence the strategy used by marine crustaceans in contests (Smith & Taylor, 1993). Aggressive and defensive behaviours control social interactions (Schone, 1968) and factors (*i.e.* population density, competition, predation, mating frequency, moult stage) influence social and mating behaviours in marine crustaceans (see review in Caldwell & Dingle, 1977).

Dingle (1983) summarized three criteria needed for the evolution of agonistic behaviours in Crustacea: (1) resources must be worth defending, (2) resources must be defendable (*i.e.* occupied or confined), and (3) individuals must have the ability and need for defence of the resource. Most crustaceans are excellent model organisms to study the evolution and function of aggressive behaviours because (1) they make formidable opponents by possessing spines, chelae, or claws, (2) they occupy defendable 'homes' that vary in energy expended for construction or defence, such as shells, burrows, or cavities, and (3) many species can be maintained in the laboratory due to their small size and can also be observed in the natural habitats. Agonistic behaviours of many crustaceans have been studied (crayfish: Bovbjerg, 1956; brachyuran crabs: Schone, 1968; snapping shrimp: Schein, 1975; hermit crabs: Hazlett, 1978; stomatopods: Caldwell & Dingle, 1979).

Mantis shrimp, also called stomatopods, are active predatory, marine, bethic crustaceans that exhibit complex quantifiable behaviours, which may not differ between the sexes (Caldwell, 1992). The variable assortment and complexity of agonistic behaviours and interactions in mantis shrimp appear to be related to their habitat as well as their feeding methods. There is variation in agonistic behaviours and their functions among families and species (Dingle & Caldwell, 1975).

Stomatopods are divided into two functional groups, smashers and spearers, based on differences in morphology, habitat, and behaviour. Caldwell (1991) summarized the main differences in behaviour, habitat, and ecology between these groups. Generally, smashers are more cavity limited and have evolved more complex agonistic and mating behaviours than spearers. Smashers and spearers differ in the morphology and use of the raptorial appendage; smashers have an enlarged heel of the dactyl and use it to kill hard-bodied prey, whereas spearers use teeth on the dactyl to kill soft-bodied prey (see Table 1 for summary). Because stomatopods are active, these taxa have provided scientists with a system to study agonistic interactions, specifically intraspecific interactions related to limiting resources such as cavities or burrows.

Stomatopods are sensitive to differences in individual strength and size (Caldwell & Dingle, 1979; Adams & Caldwell, 1990). Larger individuals are usually stronger, more experienced, and have the potential to inflict greater injury in a dispute. Stomatopods have indeterminate growth, which suggests that interacting adults vary in body size in their natural habitats. Thus, the probability of a successful agonistic interaction is related to an individual's relative aggressive level and size. Most studies of intrasexual and intersexual agonistic interactions in smashers have been in respect to body size, and few studies have quantified the agonistic behaviours of spearers (Dingle & Caldwell, 1975, 1978; Caldwell & Dingle, 1975) (see Table 2 for summary).

Squilla empusa Say, a spearer mantis shrimp, is distributed in the mud and sandy bottoms of the Atlantic Ocean from Maine, U.S.A. to Surinam, South America and in most of the Gulf of Mexico (Manning, 1969). It excavates and inhabits burrows constructed out of a combination of sand and mud and occurs in high salinity waters (Franks *et al.*, 1972).

Sqiulla empusa ranges in total length from 28.7-165.0 mm for males and 33.8-185.0 mm for females (Manning, 1969). Rockett *et al.* (1984) collected individuals that ranged from 26-132 mm in total length and found

TABLE 1. *General comparison and summary of typical characteristics of smasher and spearer stomatopods*

Characteristic	Smasher	Spearer	Reference
Burrow type	Pre-existing hard substrate — coral and rock	Self-excavated — mud and sand	Caldwell, 1991
Burrow abundance	Limited by sheer numbers	Limited by energy to construct	Caldwell, 1991
Common depth	0-20 m	50-100 m	Abbott *et al.*, 1984
Light	Bright	Dim	Caldwell, 1991
Water clarity	Clear	Turbid	Caldwell, 1991
Body color	Bright	Dull	Abbott *et al.*, 1984
Meral spread display	Common	Rare	Dingle & Caldwell, 1975
Meral spot	Bright colors	Dull colors	Abbott *et al.*, 1984
Activity	Active in day	Active at night; in day, only to forage	Caldwell, 1991
Light rays	Funneled into rhabdom	Not funneled	Abbott *et al.*, 1984
Ommatidia	Very skewed	Barely skewed	Abbott *et al.*, 1984
Prey type	Hard-armored animals	Soft-bodied animals	Caldwell, 1991

statistically significant differences between male and female body sizes once larger size was obtained, with females being larger. Most females spawn in an 8-month period from January to August; however, a few gravid females were collected from September to December (Rockett *et al.*, 1984; pers. obs.).

Myers (1979) determined for northern populations of *Squilla empusa* that burrows differed between winter and summer months with vertical winter burrows (about 4.1 m) consisting of one opening and horizontal summer burrows (about 2 m) having two similar sized openings. Myers (1979) & Frey & Howard (1969) reported that populations as far south as Georgia (USA) have similar burrows all year, and the burrows have at least two openings.

TABLE 2. *Summary of research on intraspecific mantis shrimp behaviours*

Species	MM	FF	MF	Size matched	Different sizes	Cavity defence	Open arena	Reference
*Cloridopsis scorpio**	X	X		X		N	X	1)
Gonodactylus bredini	X	X	X	X	X	A, N	X	2)
Gonodactylus festae	U	U	U		X	A		Caldwell, 1985
Gonodactylus festai	X	X		X		A	X	Caldwell, 1979
Gonodactylus incipiens	X	X	X	X		N	X	Dingle *et al*., 1973
Gonodactylus oerstedi	X	X	X	U	U	N		Dingle & Caldwell, 1966
Gonodactylus spinulosus	X	X		X			X	Dingle, 1983
Gonodactylus viridis	X	X		X	X		X	Caldwell & Dingle, 1979
Gonodactylus zacae	X				X		X	3)
*Haptosquilla glyptocercus**	X	X	X	X		X	X	4)
*Oratosquilla inornata**	X	X		X		N	X	5)

For many studies, the methods reported that intersexual interactions were conducted, but they were not reported in the results or discussion. Also, for many studies, the type of encounters that were staged is unclear in the methods; but upon reading the results, it appears that both size matched and different sized matched interactions occurred. MM = male-male interactions; FF = female-female interactions; MF = male-female interaction; U = unclear or unable to tell from methods what type of tests conducted; * = spearer mantis shrimp; N = natural burrow made from coral/rock substrate or animal self-excavated in sediment; A = artificial burrow used of glass flask, concrete, or PVC pipe.

Note: 1)Dingle & Caldwell, 1975, 1978. 2)Dingle, 1969; Dingle & Caldwell, 1969; Dingle & Caldwell, 1972; Shuster & Caldwell, 1982; Berzins & Caldwell, 1983; Steger & Caldwell, 1983; Dingle, 1983; Montgomery & Caldwell, 1984; Shuster & Caldwell, 1989; Adams & Caldwell, 1990; Caldwell, 1992. 3)Caldwell, 1972; Reaka, 1972. 4)Dingle *et al.*, 1973; Caldwell & Dingle, 1977. 5)Dingle & Caldwell, 1975, 1978.

The purpose of this study, using a species of spearer mantis shrimp, *Squilla empusa*, was to engage size-matched individuals and study the interactions and behaviours between same-sex and opposite-sex individuals. The main objective was to determine behavioural differences between males and females, without the variable of body size asymmetries.

The predictions of this study were that (1) *Squilla empusa* should rarely display but have frequent, physically aggressive, interactions. The rationale for this prediction is that most spearers have poor vision, dull meral spots, and live in deep, murky waters, all of which make assessment of others difficult (Caldwell, 1991). (2) Males and females are equally aggressive. There should be equal numbers of interactions between same-sexed individuals and

opposite-sex individuals. The rationale for this prediction is that spearers have little ability to assess their opponents (due to murky habitat, dull meral spot morphology, and little sexual dimorphism). Individuals may need physical contact in order to assess their opponents. (3) An increase in the number of treatment individuals should lead to an increased number of interactions, just based on an increased chance of encountering another shrimp.

Methods

Collection and laboratory methods

In the Gulf of Mexico off the coasts of Louisiana, Mississippi, and Alabama, I collected *Squilla empusa* at night in June 1997 and June 1998 using shrimp trawls aboard the R/V *Tommy Munroe* (Southeast Area Monitoring and Assessment Program — SEAMAP cruises). These organisms live in high densities, and over 100 individuals can be collected during a 30-min trawl. The shrimp were transported back to The University of Louisiana at Lafayette in collecting bags with oxygenated seawater. Shrimp were housed individually, in order to prevent agonistic behaviours and cannibalism, in containers 32 × 16 × 9 cm that were submerged in a round aquaculture tank (approximately 5678 L). Individuals were fed peeled penaeid shrimp, and water temperature ranged from 21-23°C with a photoperiod of 14L : 10D, while salinity ranged from 30-33 ppt. Because Manning (1969) determined that carapace length (CL) was an accurate estimate of total length, each animal was sexed and CL was measured. Individuals were sexed by identifying the penes on males at the base of the 8th walking appendage and a modified 6^{th} ventral thoracic segment with a seminal receptacle on females. Because injuries impact fighting behaviour (Berzins & Caldwell, 1983), only animals with both raptorial appendages were used.

Squilla empusa constructs natural burrows of a longer length (about 2 m) than provided in these laboratory experiments (40.6 cm) (Myers, 1979). The laboratory constraint of using polyvinyl chloride (PVC) as artificial burrows, however, did not seem to influence the behaviour of the mantis shrimp. Many previous studies have used artificial burrows in the laboratory to simulate burrow/territory quality (plastic bottles with the smasher *Gonodactylus festai*: Caldwell, 1979, *Gonodactylus bredini*: Berzins & Caldwell, 1983, *Gonodactylus festae*: Caldwell, 1985; Erlenmeyer flasks with the smasher *Gonodactylus falcatus*: Reaka, 1980, smasher *Gonodactylus bredini*: Dingle & Caldwell, 1969, 1972; spearers *Oratosquilla inornata* and *Cloridopsis scorpio*: Dingle & Caldwell, 1975, 1978; PVC pipe with the spearer *Oratosquilla oratoria*: Matsuura & Hamano, 1984). In all of the species above and in my preliminary observations of *Squilla empusa*, individuals accepted artificial burrows and appeared to treat them as natural burrows (*i.e.* by defending them from invaders, returning to them with provided food, cleaning excess food from them, and brooding eggs in them). The PVC burrow used in this study had two-openings, similar to southern natural burrows.

Experimental design

I examined intrasexual and intersexual interactions among intermoult individuals. To examine the role of sexual interactions in agonistic behaviours, each test animal was presented with a

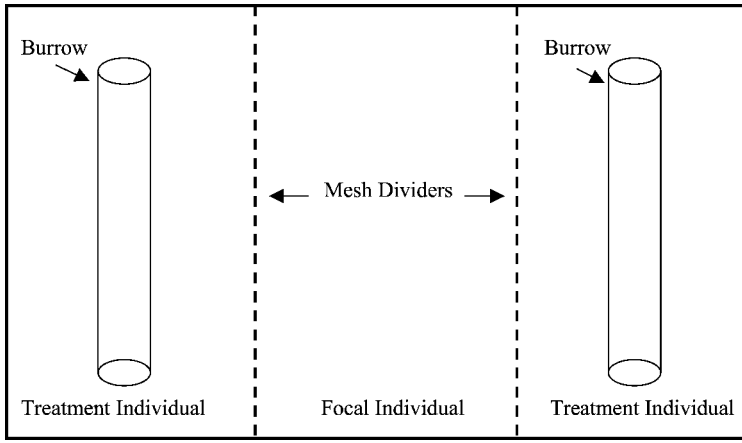

Fig. 1. Experimental test arena. Treatment individuals corresponding to treatments 1-5 and 7-11 were placed in the left and/or right chambers. The focal animal was placed in the middle chamber. Black mesh dividers divided the chambers and were removed after a one-hour acclimation period.

series of six different treatments (6 treatments = 1 trial, described below). Altogether, 300 interactions among 50 shrimp (25 males and 25 females) were observed for a total of 450 hours. The entire test arena was 626 × 635 × 127 cm and was divided into three chambers by using dark mesh dividers, which allowed water flow but prevented direct contact between individuals. Two artificial burrows were placed in the test arena, one at each end of the test area (side A and side B) (Fig. 1). The burrow sizes were selected based on a regression equation that predicts preferred burrow size (mm) from CL (my unpublished data). Before the dividers were removed, focal and treatment individuals were allowed to acclimate for 1 h in the chamber, which was enough time to establish ownership of a burrow (Caldwell, 1979; Shuster & Caldwell, 1989).

Focal animals (N_{male} = 25, N_{female} = 25) were randomly selected and placed in the middle chamber, while individuals corresponding to one of the six treatments were placed in the left and right chambers (Table 3). Individuals were randomly placed in right and left chambers, and treatment order was randomised. Each focal animal was randomly tested in 6 treatments (male: treatments 1-6, females: treatments 7-12). Treatment individuals were residents of burrows, while focal animals represented animals without burrows. To control for body size effects, all individuals used in each trial differed less than 10% in body size (Caldwell, 1979; Caldwell & Dingle, 1979). Each organism was fed one day before being tested, and an individual was used only once in each trial (6 treatments = 1 trial) to control for recognition and learned behaviours (Caldwell, 1979, 1992).

Behaviours were based on those defined by Dingle (1969, 1972) and Dingle & Caldwell (1969). An 'act' is the performance of a single specific behaviour by a single individual. A 'strike' is a blow delivered by one individual to another individual using the dactylus of the raptorial appendage and is the most obvious aggressive act. In my study, the dactyl always remained folded and no individual ever struck an opponent with the spear end of the raptorial appendage. 'Meral spread/display' is the outward spreading of the raptorial appendage.

TABLE 3. *Treatments for focal male and focal female individuals*

Treatment/Individual	Left	Middle/Focal animal	Right	*N*
Treatment 1	Male	Male	Female	25
Treatment 2	–	Male	Male	25
Treatment 3	–	Male	Female	25
Treatment 4	Male	Male	Male	25
Treatment 5	Female	Male	Female	25
Treatment 6 (Control)	–	Male	–	25
Treatment 7	Male	Female	Female	25
Treatment 8	–	Female	Male	25
Treatment 9	–	Female	Female	25
Treatment 10	Male	Female	Male	25
Treatment 11	Female	Female	Female	25
Treatment 12 (Control)	–	Female	–	25

Treatment individuals were placed in the left and/or right side of the test area, and this procedure was done using a random numbers table to determine which individual went into each side for every treatment.

'Activity level' was determined by how many times the focal animal crossed a boundary line from the left, middle, or right chambers of the test arena. Every time that the focal animal moved across a boundary line, this counted as one movement. An 'interaction' occurred when two individuals met each other and some physical contact was made. A 'passive' behaviour occurred when two individuals interacted but did not resort to aggressive striking behaviour.

Contest duration influences fighting behaviours in stomatopods. After a short time, interactions between two individuals decrease (Adams & Caldwell, 1990). Dingle (1969) reported the most aggressive behaviours occur within the first 20 min of a 60-min contest, and activity level and frequency of agonistic acts decline toward the end of a contest. More aggressive acts (*i.e.* strikes) occur in interactions with cavities/burrows rather than in open arena contests (Dingle & Caldwell, 1975). Thus, I used a burrow experimental design, instead of the open arena. I recorded the following behaviours associated with agonistic interactions for 30 min and then at four periodic observations over the next 60 min: (1) 'activity level' (number of movements) of the focal animal in each treatment, (2) the number of 'strikes' by treatment individuals and by focal animals, (3) the total number of interactions between a focal animal and a treatment individual, and (4) the result of an interaction (the contest lead to a 'strike' or to 'passive' behaviour).

Statistical analyses

The purpose of this study was to determine if there are intrasexual differences in agonistic behaviours related to body size (CL) in *Squilla empusa*, as well as to uncover any intersexual differences in agonistic behaviours. Many different statistical tests were needed to compare intrasexual and intersexual behaviours and to test for relationships of specific behaviours to body size. All statistical analyses were conducted using SAS software (SAS Institute, Inc., 1999) and Siegel & Castellan (1988). A Shapiro-Wilkes test for normality was conducted

on all data in order to determine if normality assumptions were met. If normality assumptions were met, parametric statistics were used. If normality assumptions were not met, then transformation of the data set was attempted. If the transformation did not improve normality, then nonparametric statistics were used. Multiple comparisons are reported only for significant tests ($\alpha = 0.05$). Because of the exploratory nature of this experiment, alpha values were not reduced (Jaeger & Halliday, 1998).

Size and burrow analyses

A t-test was conducted to determine if focal males ($N = 25$) and females ($N = 25$) differed in body sizes. To determine if males and females occupied burrows at equal frequencies, the number of individuals (treatment and focal animals) that entered a burrow and occupied it was recorded and a chi-square test was used. Next, the treatment in which the focal individual entered a burrow the fastest was recorded. A chi-square analysis was conducted separately for each sex of focal animal to determine if the sex of treatment individuals influenced the rate that focal animals gained ownership of a burrow.

Activity level analyses

A Spearman correlation analysis was used to determine if the total number of movements in a trial (6 combined treatments) was related to focal animal's size (CL) ($N_{\text{males}} = 25$, $N_{\text{females}} = 25$). In order to determine if focal females differed from focal males in activity level, a Wilcoxon signed ranks test ($N = 25$) was performed, which controlled for body size. In this test, males and females were size matched. Friedman's nonparametric analyses were used to determine if male and female focal animals differed in activity level when placed with the same combination of treatment individuals.

Interaction analyses

Because there were no individuals with which the focal animal could interact in treatments 6 and 12, these treatments were not included in these analyses. Linear regression analyses were conducted on the total number of interactions in a trial with CL (for both focal males and females). Because males and females were statistically different in body size, data for males and females were analysed separately.

The number of contacts that occurred between two individuals (a focal animal and a treatment individual) in a trial was recorded and analyzed using a t-test ($N_{\text{male}} = 25$, $N_{\text{female}} = 25$). The number of intrasexual interactions in all treatments combined ($N_{\text{total}} = 50$; $N_{\text{mm}} = 25$, $N_{\text{ff}} = 25$) was compared to the number of intersexual interactions in all treatments combined ($N_{\text{total}} = 50$; $N_{\text{mf}} = 25$, $N_{\text{fm}} = 25$) using a t-test. The combined numbers of focal male-male (M-M) and focal female-female (F-F) interactions were compared with the combined data of focal female-male (F-M) and focal male-female (M-F) interactions. Next, I determined if the number of focal M-M interactions differed in frequency from focal F-F interactions. A Kruskal-Wallis test was used to determine if focal females and focal males interacted differently when placed with treatment females and treatment males.

The total number of interactions by each focal animal in each treatment was recorded and a Friedman's analysis was used to test if focal animals ($N_{male} = 25$, $N_{female} = 25$) differed in their interactions among the six treatments; post-hoc multiple comparison tests were conducted on significant tests. It was also documented if an interaction lead to aggressive behaviour (a strike) or passive behaviour (one-tailed Wilcoxon signed-rank tests; statistical sample size was reduced from 25 to 20 or 22, depending on individuals tested, due to tied scores).

Aggressive agonistic behaviour analyses

A Spearman' correlation was used compare the total number of strikes in a trial with the size (CL) for each focal animal (excluding the control: treatments 6 and 12). A Friedman's analysis was used to determine if the total number of strikes varied among the 5 treatments. A Kruskal-Wallis analysis tested if male focal animal treatments had more strikes than female focal animal treatments.

I recorded the number of strikes towards a focal animal by a treatment individual. A Spearman's correlation analysis was conducted to determine if the number of attacks on focal animals was significantly related to focal animal body size. A polynomial regression on female data was conducted.

The number of males striking a female (M-F), males striking a male (M-M), females striking a female (F-F), and females striking a male (F-M) was documented and analysed using a Friedman's test. In these analyses, data from the different treatments were combined, excluding the controls. A Kruskal-Wallis test was used to determine if the number of intersexual and intrasexual aggressive behaviours differed between male and female focal trials.

Results

Size and burrow analyses

Males were significantly smaller than females (Table 4A). The frequency of burrow ownership did not differ significantly between males and females (Table 4B). Sex of treatment animals (the main variable among treatments) did not significantly influence the fastest time that focal individuals entered burrows (male: df = 5, $\chi^2 = 5.64$, $p = 0.90$; female: df = 5, $\chi^2 = 3.0$, $p = 0.90$).

Activity level analyses

Larger males moved more than smaller males (Fig. 2; Table 5A). However, the number of movements was not significantly correlated with focal female body size (Table 5B). Focal males and females did not significantly differ in their activity level in a trial (Table 5C).

TABLE 4. *Do males and females have equal body sizes and occupy burrows at equal frequencies? Body size and burrow occupation differences between males and females of Squilla empusa in all trials (1 trial = 6 treatments)*

Null hypotheses	Means		df	Statistic	p
	Male	Female			
(A) No significant difference between male and female body size (CL)	18.2 mm	19.6 mm	48	$t = -2.49$	0.002
(B) No significant difference in the frequency of burrow occupation between males and female treatment[1)] and focal individuals[2)]	41[1)]	26	1[1)]	$\chi^2 = 3.36$[1)]	0.10[1)]
	20[2)]	15	1[2)]	$\chi^2 = 0.71$[2)]	0.90[2)]

Note: t = t-test; χ^2 = chi-square test; df = degrees of freedom.

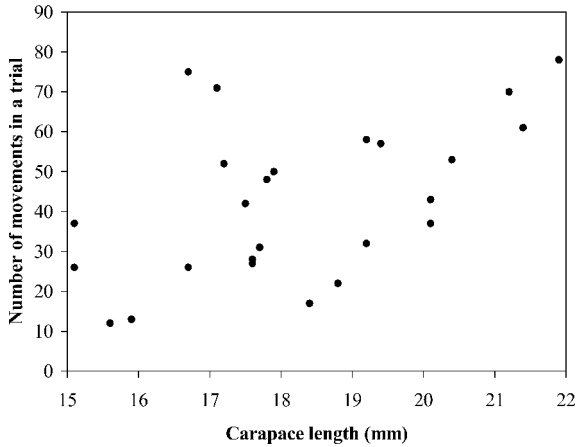

Fig. 2. Activity level of male focal animals. Spearman correlation coefficient $r_s = 0.48$, $p = 0.02$.

Focal male activity level significantly differed among the six treatments (Table 5D). Focal males in treatment 4 (M-M) moved significantly more than in treatment 6 (control) ($p < 0.05$, number of comparisons =15). Focal female activity level also significantly differed among the six treatments (Table 5E). Focal females in treatments 9 (F-), 10 (M-M), and 11 (F-F) had significantly more movements than focal females in the control (treatment 12) ($p < 0.05$, number of comparisons = 15). Male and female focal animals did not show a difference in activity level when placed with the same combination of treatment individuals (Table 6).

TABLE 5. *Is activity level related to the body size of the individual? Do males and females have equal activity levels? Does activity level differ among the different treatments? Differences in activity level between focal males and females*

Null hypotheses		Medians	df	Statistic	p
(A)	No significant correlation between activity level in a trial and male carapace length (mm)			$r_s = 0.48$	0.02
(B)	No significant correlation between activity level in a trial and female carapace length (mm)			$r_s = 0.27$	0.20
(C)	No significant difference between male and female activity level in a trial	Male: 42.0 (30) Female: 32.0 (33)		$T^+ = 170$	0.42
(D)	No significant difference in male activity level among the 6 treatments (t1-t6)	Median: t1 = 7 (8) t2 = 7 (7) t3 = 5 (7) t4 = 7 (8) t5 = 5 (4) t6 = 3 (5)	5	$F_r = 12.3$	<0.05
(E)	No significant difference in female activity level among the 6 treatments (t7-t12)	Median: t7 = 3 (8) t8 = 4 (8) t9 = 5 (6) t10 = 9 (12) t11 = 9 (11) t12 = 3 (4)	5	$F_r = 22.6$	<0.001

'Activity level' is the number of movements an individual made across a boundary line (left, middle, and right sides) in the test arena. Every time an individual crossed a boundary line, this counted as one movement. 1 trial = 6 treatments. Interquartile range is in ( ).
Note: r_s = Spearman's correlation coefficient; T^+ = Wilcoxon Sign ranks test; F_r = Friedman's two-way analysis of variance by ranks test; df = degrees of freedom; t = treatment.

Interaction analyses

The total number of interactions in a trial was not influenced by body size (males: $p = 0.25$; females: $p = 0.67$). Male and female focal individuals significantly differed in number of interactions; males were involved in more interactions than females (Table 7A). Same-sex individuals interacted about the same number of times as opposite sex individuals (Table 7B). More focal male-male interactions occurred than focal female-female interactions (Table 7C). Focal animals behaved similarly with regard to the number of interactions with members of the opposite sex (Table 7D).

TABLE 6. *Do males and females have equal activity levels when comparing similar treatments? Comparison of female and male focal activity level in each of the 12 treatments, using Kruskal-Wallis analyses*

Treatment	Male		Female		N	χ^2	df	p
	Median	IQR	Median	IQR				
1 *vs* 7	7	8	3	8	50	1.81	1	0.18
2 *vs* 8	7	7	4	8	50	0.59	1	0.44
3 *vs* 9	5	7	5	6	50	0.12	1	0.73
4 *vs* 10	7	8	9	12	50	1.19	1	0.27
5 *vs* 11	5	4	9	11	50	2.26	1	0.13
6 *vs* 12	3	5	3	4	50	0.01	1	0.90

'Activity level' is the number of movements across boundary lines in the test arena (from left, middle, and right). The treatments compare focal male and females with the same sex treatment individuals; Table 3 describes treatment individuals. Median values are the number of movements of focal animal in the treatment. 'IQR' is the interquartile range for each treatment.

TABLE 7. *Do males and females have equal numbers of interactions? Are there an equal number of intrasexual and intersexual interactions? The differences in the number of interactions between focal male and female individuals*

Null hypotheses		Means (SE)	df	Statistic	p
(A)	No significant difference in the number of interactions between focal males and females	Male: 16.3 (0.07) Female: 10.9 (0.07)	48	$t = 1.98$	0.05
(B)	No significant difference in the number of intrasexual and intersexual interactions	Inter: 6.08 (0.03) Intra: 6.61 (0.02)	98	$t = -0.45$	0.65
(C)	No significant difference in the number of M-M and F-F interactions	M-M: 8.22 (0.05) F-F: 5.17 (0.04)	48	$t = 2.10$	0.04
(D)	No significant difference in the number of M-F and F-M interactions	M-F: 7.08 (0.07) F-M: 5.17 (0.06)	48	$t = 1.09$	0.28

An 'interaction' is when two individuals met each other and some physical contact was made. 'SE' is standard error.

Note: t = t-test; df = degrees of freedom; M-M = male focal animal interacted with a male treatment individual, F-F = female focal animal interacted with a female treatment individual, M-F = male focal animal interacted with a female treatment individual, F-M = female focal animal interacted with a male treatment individual.

TABLE 8. *Does the number of interactions differ among the different treatments? Differences in the number of interactions in each treatment between focal males and females*

Null hypotheses		Medians	df	Statistic	p
(A)	Focal males have an equal number of interactions among the 5 treatments (t1-t5)	t1 = 3.0 (4) t2 = 1.0 (3) t3 = 1.0 (3) t4 = 4.0 (5) t5 = 4.0 (4)	4	$F_r = 13.5$	<0.01
(B)	Focal females have an equal number of interactions among the 5 treatmentst (t7-t11)	t7 = 2.0 (3) t8 = 1.0 (1) t9 = 2.0 (3) t10 = 2.0 (6) t11 = 2.0 (2)	4	$F_r = 11.0$	<0.05

An 'interaction' is when two individuals met each other and some physical contact was made. Treatment 6 and 12 were not included in the analyses because there were not any other individuals for the focal animal to interact. Interquartile range is in ( ).

Note: F_r = Friedman's two-way analysis of variance by ranks test, t = treatment number.

Focal males and females did not differ significantly in the number of interactions with treatment females (male median = 7.0, female median = 5.0, $\chi^2 = 0.95$, df = 1, $p = 0.33$). Focal males had significantly more interactions with treatment males than did focal females (male median = 8.0, female median = 3.0, $\chi^2 = 4.30$, df = 1, $p = 0.04$).

For focal males, the greatest number of interactions occurred when focal males were placed with two treatment individuals, regardless of sex (Table 8A). Treatment 3 (F-) had significantly fewer ($p < 0.05$, number of comparisons = 10) interactions than treatments 1 (M-F), 4 (M-M), and 5 (F-F) (Table 8A). Focal females had the fewest interactions when placed with only one male (Table 8B). Treatment 8 (M-) had significantly fewer ($p < 0.05$, number of comparisons = 10) interactions than treatments 10 (M-M) and 11 (F-F) (Table 8B).

Female intrasexual and intersexual interactions were significantly more likely to be passive ('nonstriking') than aggressive ('striking') (Table 9). In male-male interactions, there was no significant difference in the number of passive and aggressive behaviours.

TABLE 9. *Are same sex interactions more likely to lead to an aggressive outcome? Are opposite sex interactions more likely to lead to a passive outcome? Focal animal response to specific types of interactions*

Focal animal sex	Treatment individual sex	Outcome/Behavior	N	T^+	p
Male	Male	Strike = No strike	20	137.5	0.11
Male	Female	No strike	22	71	0.04
Female	Male	No strike	23	40.5	0.002
Female	Female	No strike	23	65	0.01

An interaction that resulted in passive actions is referred to as 'no strike', whereas an interaction that resulted in an aggressive act is referred to as "strike". Statistical samples sizes eere reduced from 25 due to ties in data.

Note: T^+ = Wilcoxon signed ranks test.

Aggressive agonistic behaviour analyses

Neither larger focal males nor females were more likely to strike treatment individuals during a trial compared to smaller focal individuals (Spearman's correlation, males: $p = 0.76$; females: $p = 0.76$). The number of strikes varied among the six focal male treatments (Table 10). Focal males were significantly more likely to strike when presented with two treatment males (treatment 4) than one female (treatment 3) (multiple comparison test: $p < 0.05$, two-tailed test) (Table 10A). The number of strikes did not significantly differ among the other treatments (Table 10A). Focal females did not significantly differ in the total number of strikes among the five treatments (Table 10B). Focal males had significantly more total strikes per trial than focal female (Table 10C). Focal males attacked both male and female treatment individuals more than did focal females (Table 10D, 10E).

Focal animal body size did not significantly influence the frequency that treatment individuals attacked focal animals; large and small focal animals were attacked similarly by treatment individuals (Spearman's correlation, focal males: $p = 0.83$; focal females: $p = 0.79$). There was a significant curvilinear relationship (in the polynomial analysis of $y = x^3$) between the total strikes in a trial directed at focal females and the focal females' body sizes (carapace^3: df = 1, 21, $F = 4.30$, $p = 0.05$) (Fig. 3).

In focal male and female trials, there was a significant difference in the frequency of striking the different sexes (M-M, M-F, F-F, F-M) (male: df = 3, $F = 38.2$, $p < 0.001$; female: df = 3, $F = 11.1$, $p < 0.02$). Males and females were more likely to be attacked by males than females in

TABLE 10. *Does the use of aggressive behaviours differ among the treatments? Do males and females use aggressive behaviours equally? Striking behavior of test and focal animals (total strikes in a treatment)*

Null hypotheses	Medians	df	Statistic	p
(A) No significant difference in the total number of strikes among the 5 treatments (t1-t5) for male focal animals	t1 = 3 (6) t2 = 0 (2) t3 = 0 (1) t4 = 2 (4) t5 = 2 (4)	4	$F_r = 14.3$	<0.01
(B) No significant difference in the total number of strikes among the 5 treatments (t7-t11) for female focal animals	t7 = 0 (2) t8 = 0 (1) t9 = 0 (2) t10 = 1 (4) t11 = 1 (2)	4	$F_r = 6.18$	>0.20
(C) No difference in the total number of strikes in a trial between focal males and females	Male = 11.0 (11) Female = 6.0 (5)	1	$\chi^2 = 8.28$	0.004
(D) No difference in the total number of strikes at female treatment individuals between focal male and female individuals	Male = 2.0 (5) Female = 0.0 (2)	1	$\chi^2 = 4.48$	0.03
(E) No difference in the total number of strikes at male treatment individuals between focal male and female individuals	Male = 3.0 (5) Female = 1.0 (1)	1	$\chi^2 = 4.41$	0.04

A 'strike' is a blow delivered by one individual to another individual using the dactylus of the raptorial appendage and is the most obvious aggressive act. Treatments 6 and 12 were not included in any analyses because there was no other individual to participate in an aggressive encounter. Focal animals never performed a strike in treatment 6 or 12. 1 trial = 5 treatments. Interquartile range is in ( ).

Note: F_r = Friedman's two-way analysis of variance by ranks test, t = treatment number; χ^2 = Kruskal-Wallis test; t = t-test; df = degrees of freedom.

focal male trials (male and female, $p < 0.05$). There were significantly more male-male striking encounters than female-female encounters in both focal male and focal female trials (focal male and focal female, $p < 0.05$). Focal females and focal males trials had similar numbers of intersexual aggressive encounters (M-F or F-M) (Table 11).

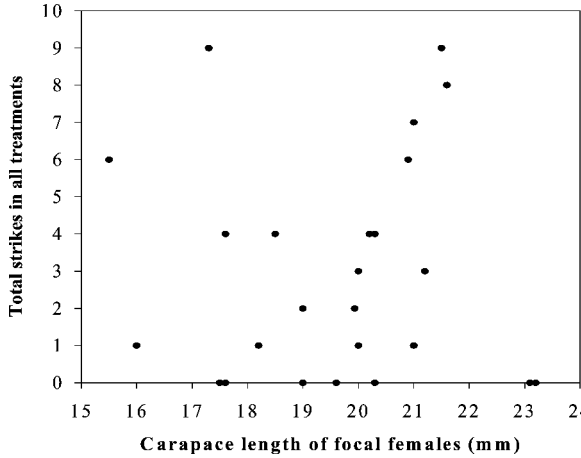

Fig. 3. Polynomial regression analysis on the total number of strikes directed at a female focal animal as a function of carapace length (carapace^3: df = 1, 21, $F = 4.30$, $p = 0.05$).

TABLE 11. *Do focal males and focal females strike opposite-sex individuals equally? The differences in intersexual striking interactions in focal male and focal female trials*

Striking interaction		Focal male		Focal female		χ^2	p
		Median	IQR	Median	IQR		
(A)	Any male strikes any female when focal animal was:	2	3	1	2	3.19	0.07
(B)	Any female strikes any male when focal animal was:	1	2	1	2	0.0036	0.95

A 'strike' is a blow to another individual using the raptorial appendage and is the most aggressive act. Statistics given are the median number of strikes in a trial with a focal male or female. 'IQR' is the interquartile range. A Kruskal-Wallis test was used. (A) = total strikes by males in treatments 1, 3, 5, 7, 8, and 10. (B) = total strikes by females in treatments 1, 3, 5, 7, 8, and 10.

Discussion

Summary of results

The purpose of this study was to test for size and sex differences in specific behaviours and their frequency of use. There are several conclusions that can be drawn from the results. (1) Any interactions involving a female

(F-F, F-M, M-F) were more likely to lead to passive, non-aggressive behaviours, whereas, male-male interactions had an equal likelihood of leading to aggressive or non-aggressive behaviours. (2) The number of intersexual (M-F + F-M) interactions were similar to the number of intrasexual (M-M + F-F) interactions; however, males (M-M) engaged in more intrasexual interactions than females (F-F). (3) Focal males were involved in more interactions and strikes (with treatment individuals) than focal females. (4) Males participated in more interactions and more aggressive behaviours with other males than did females. (5) While males are generally more aggressive than females, males and females participated in similar numbers of intersexual aggressive acts. (6) There was no relationship between the number of interactions or the number of strikes for either sex and body size. Larger individuals engaged in similar numbers of interactions as smaller and intermediate sized individuals, and larger individuals were attacked similarly to smaller individuals. (7) There was a relationship between the number of interactions and the number of individuals in the treatment. The treatments with only one treatment individual (treatments 2, 3, 8, 9) had fewer interactions than treatments with two treatment individuals (treatments 1, 4, 5, 7, 10, 11). (8) Males and females did not differ in their activity levels, regardless of body size or treatment. (9) Larger males moved more than smaller males. (10) Males and females occupied burrows at similar frequencies.

Inferences from results regarding spearer agonistic behaviours

Little work on the intersexual interactions of spearers stomatopods has been reported. Males of *Cloridopsis scorpio* participate in more agonistic acts than females; in *Oratosquilla nepa* and *O. inornata*, there are no agonistic differences between the sexes (Dingle & Caldwell, 1975). In my present study, there were more male-male interactions and aggressive behaviours than female-female interactions and aggressive behaviours.

There appears to be no relationship between body size and frequency of interactions for *Squilla empusa*, perhaps because spearers have less precision in their visual senses. Spearer mantis shrimp may rely on direct physical contact in order to assess other individuals, unlike smashers, which have complex vision with which to assess other individuals without direct contact (Abbott *et al.*, 1984).

Small and large focal animals had similar numbers of strikes directed at them, and there was no relationship between the number of attacks by each

sex and the size of the male or female focal animal. Smaller males were not more likely to be attacked by males than were larger individuals. Thus, body size in *Squilla empusa* may not be a good predictor of individual aggressive tendencies.

The results of male size-matched contests suggest that males have a 50% chance of being physically attacked; thus, 50% of the interactions involving two males will lead to a 'strike' and 50% will lead to 'no strike'. Any interaction involving a female is more likely to result in passive, non-striking behaviour.

Individuals, especially males, engaged in frequent aggressive striking acts. The strike has several functions; it can be used to drive opponents away from a territory, in prey capture, and in feeding. The raptorial strike can be lethal, and a single strike can inflict severe injury; thus escalated contests can be viewed as risky behaviour to both contestants (Berzins & Caldwell, 1983). Most strikes directed at individuals of the same or different stomatopod species, however do not result in severe damage and are conducted with the dactyl closed (Dingle & Caldwell, 1975; Caldwell, 1979). No damage by a raptorial strike was observed in my study. Thus, striking behaviour can be viewed as a forceful, yet non-destructive, display.

Burrow occupation did not vary significantly between the sexes. Males and females occupied burrows at similar frequencies, which suggests that burrows are resources of equal importance to both sexes.

Comparison of spearer and smasher agonistic behaviours

A main hypothesis that attempts to explain the differences in agonistic behaviours between smashers and spearers is that, because spearers are not limited by sheer numbers of burrows/cavities as are smashers, there has not been selection for the evolution of complex agonistic behaviours for cavity defence (Dingle & Caldwell, 1975). Members of the family Squillidae have been documented as having less complex behaviours and usually being less aggressive than members of the mostly smashing family Gonodactylidae. Caldwell & Dingle (1975) and Dingle & Caldwell (1975) reported that squillids are less active than smashers in number of agonistic acts and displays, avoid more interactions than smashers, and have little obvious agonistic behaviours. This study confirms the infrequent use of threat displays by a spearer mantis shrimp, but suggests that spearers may strike and interact frequently.

Caldwell & Dingle (1975) summarized the evolution of agonistic behaviours in mantis shrimp as far as the similarities and relation to habitat. Dingle & Caldwell (1975) reported that differences in body size, environmental factors, and differences in sensory structures might also impact behaviours among different species and populations of mantis shrimp. My experiment, using a spearer, supports Caldwell & Dingle's prediction that spearers, which have energy investments in their burrows, will be aggressive, yet have few complex behaviours and displays. Differences in body size, however had very little impact on agonistic behaviours in this study.

Smashers have more complex and more frequent agonistic acts and behaviours than spearers (Dingle & Caldwell, 1975). The most common display in stomatopods is meral display, which is believed to provide an opponent with information about body size and fighting ability. While many smashers use meral displays and stop intruders from invading their burrows (Dingle & Caldwell, 1969; Caldwell, 1979; Steger & Caldwell, 1983; Adams & Caldwell, 1990; Adams & Mesterton-Gibbons, 1995), other spearers and *Squilla empusa* were not observed to use the meral spread with any predictability (Dingle & Caldwell, 1969, 1978; Caldwell & Dingle, 1975, 1976; present study). While Dingle & Caldwell (1969) reported that the meral spread is an obvious act used by *Squilla empusa*, in my study, in which the agonistic acts of *Squilla empusa* were observed for 300 hours (continuous time), the act was rarely seen. These differences, between spearers and smashers, in use of meral threat displays may be related to differences in visual senses and capabilities in differentiating shapes and colors (Abbot *et al.*, 1984). Thus, spearers, whose vision is less complex than that of smashers, appear to engage in frequent interactions instead of using displays when assessing their opponents (Abbott *et al.*, 1984).

Research on interactions of male and female stomatopods is rare (Shuster & Caldwell, 1982, 1989; Montgomery & Caldwell, 1984). For smashers, few differences have been reported between males and females as far as agonistic behaviours, so data on males and females have usually been pooled (*Gonodactylus viridis*: Caldwell & Dingle, 1979; *Gonodactylus bredini*: Berzins & Caldwell, 1983; Steger & Caldwell, 1983; Adams & Caldwell, 1990; *Gonodactylus festae*: Caldwell, 1985). Other agonistic interactions between smasher males and females vary if a pair bond has formed and also vary depending on a female's reproductive condition and receptivity (Dingle & Caldwell, 1966, 1972). When members of opposite sexes did

encounter each other under non-courtship situations, the female usually attacked first (smasher species: Dingle & Caldwell, 1972), and smasher females are usually more reluctant to fight (Dingle & Caldwell, 1972; Shuster & Caldwell, 1989). Most research on agonistic interactions in mantis shrimp has been on intrasexual behaviour, although a few studies have observed interactions between males and females (see Table 2 for summary). The present study found several significant differences between male and female agonistic behaviours in the spearer, *Squilla empusa* and overall suggests that males are more aggressive than females.

Conclusions

Agonistic behaviours in mantis shrimp probably coevolved with the structure of the raptorial appendage and burrow type. The spearer raptorial appendage was initially used in prey capture, not aggression (Dingle & Caldwell, 1978). Other researchers have documented, for smasher stomatopods, that body size is a primary factor in determining the outcome of agonistic encounters with little or no difference between the behaviours of males and females. In the spearer *Squilla empusa*, males and females behave differently in agonistic interactions, with males participating in more interactions and using more aggressive acts than females. Individual body size did not influence the number of interactions or aggressive acts of focal animals. Males and females did not differ in their use of burrows or in their activity levels. The agonistic behaviour of *Squilla empusa* is different from the reports of smasher agonistic behaviour, and these differences are probably related to differences in habitat, morphology, and physiology.

References

Abbott, B.C., Manning, R.B. & Schiff, H. (1984). An attempt to correlate pseudopupil sizes in stomatopod crustaceans with ambient light conditions and behavior patterns. — Comp. Biochem. Physio. A 78, p. 419-426.

Adams, E.S. & Caldwell, R.L. (1990). Deceptive communication in asymmetric fights of the stomatopod crustacean *Gonodactylus bredini*. — Anim. Behav. 39, p. 706-716.

— — & Mesterton-Gibbons, M. (1995). The cost of threat display and the stability of deceptive communication. — J. theor. Biol. 175, p. 405-421.

Berzins, I.K. & Caldwell, R.L. (1983). The effect of injury on the agonistic behavior of the stomatopod, *Gonodactylus bredini* (Manning). — Mar. Behav. Physiol. 10, p. 83-96.

Bovbjerg, R.V. (1956). Some factors affecting aggressive behavior in crayfish. — Physiol. Zool. 29, p. 127-136.

Caldwell, R.L. (1972). The making of a winner-individual variation in the aggressive behavior of the mantis shrimp, *Gonodactylus zaeae*. — Amer. Zool. 12, p. 651.

— — (1979). Cavity occupation and defensive behaviour in the stomatopod *Gonodactylus festai*: evidence for chemically mediated individual recognition. — Anim. Behav. 27, p. 194-201.

— — (1985). A test of individual recognition in the stomatopod *Gonodactylus festae*. — Anim. Behav. 33, p. 101-106.

— — (1991). Variation in reproductive behavior in stomatopod Crustacea. — In: Crustacean sexual biology (R.T. Bauer & J.W. Martin, eds). Columbia University Press, New York, p. 67-90.

— — (1992). Recognition, signaling and reduced aggression between former mates in a stomatopod. — Anim. Behav. 44, p. 11-19.

— — & Dingle, H. (1975). Ecology and evolution of agonistic behavior in stomatoopods. — Naturwissenschaften 62, p. 214-222.

— — & — — (1976). Stomatopods. — Sci. Amer. 234, p. 80-89.

— — & — — (1977). Variation in agonistic behavior between populations of the stomatopod *Haptosquilla glyptocercus*. — Evolution 31, p. 220-223.

— — & Dingle, J. (1979). The influence of size differential on agonistic encounters in the mantis shrimp, *Gonodactylus viridis*. — Behaviour 69, p. 255-264.

Dingle, H. (1969). A statistical and information analysis of aggressive communication in the mantis shrimp *Gonodactylus bredini* Manning. — Anim. Behav. 17, p. 561-575.

— — (1972). Aggressive behavior in stomatopods and the use of information theory in the analysis of animal communication. — In: Behavior of marine animals: current perspectives in research, Volume 1. Invertebrates (H.E. Winn & B.L. Olla, eds). Plenum Press, New York, p. 126-156.

— — (1983). Strategies of agonistic behavior in Crustacea. — In: Studies in adaptation: the behavior of higher crustacea (S. Rebach & D.W. Dunham, eds). John Wiley and Sons, New York, p. 85-111.

— — & Caldwell, R.L. (1966). Aggressive, territorial, and reproductive behavior of the mantis shrimp *Gonodactylus oerstedi* (Stomatopoda). — Amer. Zool. 6, p. 503.

— — & — — (1969). The aggressive and territorial behaviour of the mantis shrimp *Gonodactylus bredini* Manning (Crustacea: Stomatopoda). — Behaviour 33, p. 115-136.

— — & — — (1972). Reproductive and maternal behavior of the mantis shrimp *Gonodactylus bredini* Manning (Crustacea: Stomatopoda). — Biol. Bull. 142, p. 417-426.

— — & — — (1975). Distribution, abundance, and interspecific agonistic behavior of two mudflat stomatopods. — Oecologia 20, p. 167-178.

— — & — — (1978). Ecology and morphology of feeding and agonistic behavior in mudflat stomatopods (Squillidae). — Biol. Bull. 155, p. 134-149.

— —, Highsmith, R.C., Evans, K.E. & Caldwell, R.L. (1973). Interspecific aggressive behavior in tropical reef stomatopods and its possible ecological significance. — Oecologia 13, p. 55-64

Franks, J.S., Christmas, J.Y., Siler, W.L., Combs, R., Waller, R. & Burns, C. (1972). A study of nektonic and benthic faunas of the shallow Gulf of Mexico off the state of Mississippi as related to some physical, chemical, and geological factors. — Gulf. Res. Rep. 4, p. 1-148.

Frey, R.W. & Howard, J.D. (1969). A profile of biogenic sedimentary structures in a Holocene barrier island-salt marsh complex, Georgia. — Trans. Gulf. Coast. Assoc. Geol. Soc. 19, p. 427-444.

Hazlett, B.A. (1978). Shell exchange in hermit crabs; aggressive or negotiation, or both? — Anim. Behav. 36, p. 1278-1279.

Jaeger, R.G. & Halliday, T.R. (1998). On confirmatory *versus* exploratory research. — Herpetologica 54, p. S64-S66.

Manning, R.B. (1969). Stomatopod Crustacea of the western Atlantic. — University of Miami Press, Miami.

Matsuura, S. & Hamano, T. (1984). Selection for artificial burrows by the Japanese mantis shrimp with some notes on natural burrows. — Bull. Japan. Soc. Sci. Fish. 50(12), p. 1963-1968.

Maynard Smith, J. (1982). Evolution and the theory of games. — Cambridge University Press, New York.

— — & Parker, G.A. (1976). The logic of asymmetric contests. — Anim. Behav. 24, p. 159-175.

Mesterton-Gibbons, M. & Adams, E.S. (1998). Animal contests as evolutionary games. — Amer. Sci. 86, p. 334-341.

Montgomery, E.L. & Caldwell, R.L. (1984). Aggressive brood defense by females in the stomatopod *Gonodactylus bredini*. — Behav. Ecol. Sociobiol. 14, p. 247-251.

Myers, A.C. (1979). Summer and winter burrows of a mantis shrimp, *Squilla empusa*, in Narragansett Bay, Rhode Island (USA). — Estu. Coast. Mar. Sci. 8, p. 87-98.

Parker, G.A. (1974). Assessment strategy and the evolution of fighting behavior. — J. theor. Biol. 47, p. 223-243.

Pool, R. (1995). Putting game theory to the test. — Science 267, p. 1591-1593.

Reaka, M.L. (1972). Behavior of the mantis shrimp, *Gonodactylus zacae*, from populations in isolation and in sympatry with congeners. — Amer. Zool. 12, p. 647.

— — (1980). Geographical range, life history patterns, and body size in a guild of coral-dwelling mantis shrimp. — Evolution 34, p. 1019-1030.

Rockett, M.D., Standard, G.W. & Chittenden Jr, M.E. (1984). Bathymetric distributions, spawning periodicity, sex ratios, and size compositions of the mantis shrimp, *Squilla empusa*, in the northwestern Gulf of Mexico. — Fish. Bull. 82, p. 418-426.

SAS Institute Inc. (1999). SAS Documentation for BIOL 575: Statistical ecology (First Edition, Volumes 1 and 2). — Cary, NC.

Schein, H. (1975). Aspects of the aggressive and sexual behavior of *Alpheus heterochaelis* Say. — Mar. Behav. Physiol. 3, p. 83-96.

Schone, H. (1968). Agonistic and sexual display in aquatic and semi-terrestrial brachyuran crabs. — Amer. Zool. 8, p. 641-654.

Shuster, S.M. & Caldwell, R.L. (1982). Cavity defense by pairs in the stomatopod, *Gonodactylus bredini*. — Amer. Zool. 22, p. 973.

Shuster, S.M. & Caldwell, R.L. (1989). Male defense of the breeding cavity and factors affecting the persistence of breeding pairs in the stomatopod, *Gonodactylus bredini* (Manning) (Crustacea: Hoplocarida). — Ethology 82, p. 192-207.

Siegel, S. & Castellan Jr., N.J. (1988). Nonparametic statistics for the behavioral sciences, 2nd edition. — McGraw-Hill Book Company, New York.

Smith, I.P. & Taylor, A.C. (1993). The energetic cost of agonistic behaviour in the velvet swimming crab, *Necora* (= *Liocarcinus*) *puber* (L.). — Anim. Behav. 45, p. 375-391.

Stamps, J.A. & Krishnan, V.V. (1997). Functions of fights in territory establishment. — Amer. Nat. 150, p. 393-405.

Steger, R. & Caldwell, R.L. (1983). Intraspecific deception by bluffing: a defense strategy of newly molted stomatopods (Arthropoda: Crustacea). — Science 221, p. 558-560.