

JAN 20 2010

SAINT MARY'S UNIVERSITY  
HALIFAX, CANADA  
B3H 2C3

287

*Symbiosis*, 24 (1998) 287-302  
Balaban, Philadelphia/Rehovot

## The Intraspecific Fighting Behavior of the Hawaiian Boxer Crab, *Lybia edmondsoni* – Fighting with Dangerous Weapons?

I. KARPLUS<sup>1\*</sup>, G.C. FIEDLER<sup>2</sup>, and P. RAMCHARAN<sup>3</sup>

<sup>1</sup>Department of Aquaculture, Agricultural Research Organization, POB 6 Bet-Dagan, Israel, Tel. +972-3-9683388, Fax. +972-3-9605667;

<sup>2</sup>Department of Zoology, University of Hawaii, Honolulu, HI 96822, USA;

<sup>3</sup>Southampton College, Southampton, NY 11968, USA

Received July 8, 1997; Accepted November 30, 1997

### Abstract

This study addresses the intraspecific fighting behavior of *Lybia edmondsoni*, a small xanthid crab which carries a minute sea anemone (*Triactis producta*) in each of its claws. The relationship with the anemone and its involvement as a weapon in crab contests was studied. Fifteen behavioral acts were identified, including five that were performed using anemones. Actual anemone contact between opponents was extremely rare, incidental, while other acts with anemones were performed at a distance or directed away from opponents. Three hypotheses are proposed to explain why anemones are not used as weapons during intraspecific contests. Contacts between walking legs during agonistic encounters appear to have replaced claw contacts typical for contests of xanthid crabs. Fighting behavior and claw propodus length vs. carapace width were similar for male and female crabs. Crabs were observed to split single anemones into two smaller individuals, inducing asexual reproduction in *Triactis producta*.

Keywords: Crab-anemone association, tool use, fighting behavior, *Lybia edmondsoni*, *Triactis producta*

### 1. Introduction

*Lybia edmondsoni* is a small xanthid crab endemic to Hawaii (Takeda and Miyake, 1970; Guinot, 1976) that carries a minute anemone in each chela. A

\*The author to whom correspondence should be sent.

sister species, *L. tessellata*, is found in other parts of the Western Pacific and Indian Ocean (Guinot, 1976). *L. edmondsoni* frequently carries the actinian *Triactis producta* (Cutress, 1977). Several recent taxonomic studies, including the description of new species of *Lybia* and a revision of the subfamily Polydectinae were carried out since Latreille's (1812) first description of these crabs (Ward, 1933; Sakai, 1961; Takeda and Miyake, 1970; Guinot, 1976; Tan and Ng, 1994). A total of nine different species of *Lybia* and a single species of the related genus *Polydectus* with a wide circumtropical distribution were so far described.

The first description of the association between small xanthid crabs of the subfamily Polydectinae, *L. tessellata* and *Polydectus cupilifer*, and sea anemones was published at the end of the 19th century as a small footnote to a taxonomic study of the Crustacea of Mauritius and the Seychelles Islands (Richter, 1880). *L. tessellata* was described as holding a living anemone, *Actinia prehensa*, in each of its claws by means of delicate hooks, slightly embedded in the anemone column. It was suggested that the anemone stinging cells assisted the crab in securing food and served as a defensive weapon.

The only detailed study of this association was carried out in Hawaii at the beginning of this century (Duerden, 1905). Despite the fact that this study was based on only three specimens (two of the genus *Lybia* and one *Polydectus cupilifer*), it contributed much to our understanding of the crab-anemone relationship and is still today the most important source of information. Duerden (1905), dealt with crab-anemone partner specificity, the mechanism of anemone acquisition, defensive movements carried out by the crab with its anemones, feeding behavior of the crab and anemone, as well as the cost and benefit of the association for both crab and anemone. Several reviews on partnerships between crustaceans and actinians focused on Duerden's (1905) study (Dales, 1966; Ross, 1974; Ross, 1983). However, they also stressed the need for more research on the relationship between *Lybia* and its anemones. Since anemones are used by *Lybia* for feeding and defense, this symbiosis serves as one of the best examples of tool use in all invertebrate taxa.

The purpose of the present study is to extend Duerden's (1905) work, concentrating on the here-to-fore unknown fighting behavior of *L. edmondsoni*, while paying special attention to the relationship with the anemone and its involvement as a weapon during intraspecific contests.

## 2. Materials and Methods

Fifty *Lybia edmondsoni* were collected using SCUBA at depths of 6–20 m from three inshore localities (Lanai Lookout, Blowhole, and Makaha Reef), and with mask and snorkel at one shallow water site (Kewalo Basin), on the

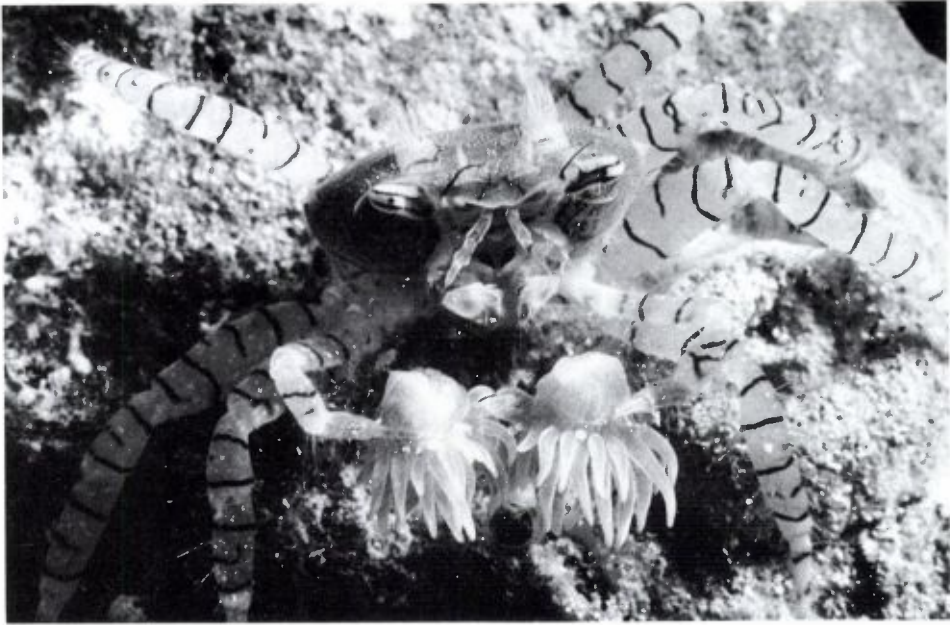


Figure 1. *Lybia edmondsoni* holding in each of its claws a *Triactis producta*.

island of Oahu, Hawaii. Crabs were found under basalt rocks and coral rubble of various sizes in these subtidal locations. Each crab held two sea anemones of the species *Triactis producta* (Fig. 1), except in two cases where crabs only carried one anemone. All crabs were sexed and measured to the nearest 0.1 mm using a vernier caliper. We defined carapace width (CW) as the linear distance between the tips of the lateral carapace spines, typical for this species.

The crabs were maintained in a wet lab at the Hawaii Institute of Marine Biology, in Kaneohe Oahu. They were kept individually in 8 l white polyethylene buckets drilled with small holes near the upper rim to facilitate water circulation. Each bucket was provided with a constant flow of seawater from Kaneohe bay at a rate of  $0.4 \pm 0.1$  l/minute per bucket. Buckets were numbered for crab identification and each was provided with a shelter. The shelters consisted of a 5 cm long PVC pipe of 5 cm in diameter, cut into half. All crabs were fed daily ad libitum either small pieces of shrimp, squid, or "fish fudge" gelatin food. Food leftovers were removed with a siphon every morning prior to feeding, and the occurrence of molts was noted. The CW of all molts was recorded and the respective crabs were re-measured. Illumination in the wet lab was provided by fluorescent lights on a 13/11 h light dark cycle, in addition to ambient sunlight. The temperature in the holding buckets ranged from 23–26°C.



Twelve pairs of crabs, six of each gender, were selected for the experiment from our captive population on the basis of size, molt state, and time spent in captivity. The average CW of experimental males and females was  $12.6 \pm 0.9$  mm and  $11.8 \pm 1.0$  m, respectively. Opponents were matched according to size, and differences (CW) between them were less than 2% in ten of the twelve pairs and less than 5% in two. All crabs were at least 7 days prior to or after ecdysis on the date of their respective contests. To minimize any handling effects crabs were in captivity at least 7 days prior to testing. Each crab was only tested once. Following testing, crabs and their anemones were sedated by slowly adding drops of 7.5%  $MgCl_2$  solution, over a period of 2 hours, to a beaker containing seawater, until the crabs became immobile.  $MgCl_2$  served to relax the anemones and prevent contraction (Cutress, 1977). The anemones were then carefully extricated from chelae using microdissection tools and preserved in 4% buffered formalin. The crabs were fixed in 10% formalin. Preserved crabs were measured again, as before, to obtain the most accurate account of CW. At this time, the claw size was also determined by recording the propodus lengths of each specimen.

As an arena for the contests served a dark green polyethylene dish, 25 cm in diameter and 4 cm in depth. The floor of the arena was roughened with a sanding wheel, then marked with a grid of 5 cm squares, to estimate motor activity and distances between individuals. Filtered, aerated sea water was used in the arena and replaced after each match. Two 8 Watt fluorescent lamps, were installed above the arena for even illumination during the contests. The arena and lamps were positioned inside a  $65 \times 70 \times 95$  cm wooden frame, and covered on all sides with black polyvinyl sheeting, in order to minimize outside stimuli during contests. A hole in the roof of the structure accommodated the lens of a JVC Super VHS video camera (Model # GR-SX90) to allow filming of crab interactions from above. During contests, the room surrounding the structure was darkened, with minor illumination from a video monitor. Inside the frame structure, the two lamps were covered with red cellophane paper. These lights provided dim illumination barely sufficient for video recording. This type of illumination was used, since the eyes of several species of crustaceans have been reported to be less sensitive to red wave lengths (Goldsmith and Fernandez, 1968; Cummins et al., 1984). Water temperature in the testing arena averaged  $23.6 \pm 1.1^\circ C$  during contests.

Contests were staged during October and November 1995. Each crab was marked for easy identification with a small strip of black plastic affixed to the dorsal surface of the carapace with a cyano-acrylate ester-based adhesive (SuperGlue). To recognize the opponents in each contest pair, one strip was oriented parallel and the other perpendicular to the body axis. Before each match, opponents were introduced into the arena in separate translucent cylinders positioned 5 cm apart inside the testing arena. After a ten minute

acclimation period, both cylinders were raised slowly and simultaneously. Crab behavior was then recorded on video-tape for 30 minutes, following the first physical contact between opponents. All contests were held at night between 21:30 and 24:00 h, when the crabs are most active (unpublished).

Behavioral acts of both opponents in each match were transcribed from video-taped encounters in a sequential order and their duration was recorded to the nearest second. Motor activity was estimated for each crab by counting the number of lines crossed on the arena grid by the frontal margin of the carapace. A bout was defined as the period of activity when the crabs were at most 5 cm apart. A bout was initiated by the approach of one or both opponents and terminated when crabs were more than 5 cm apart. The winner of each contest was defined as the crab which retreated and fled the fewer number of times.

Morphometric data of crabs (propodus length vs. body width) was examined using parametric statistics – linear regression analyses. All behavioral data were analyzed using non-parametric statistics. The Mann-Whitney U test was applied to contrast various parameters of the contests in males and females (e.g., number of acts per contest, bout duration) and the frequency that common behaviors were carried out by each sex. The Wilcoxon matched-pairs signed-ranks test was applied to contrast frequency of certain behaviors in winners and losers within each gender.

### 3. Results

#### *Morphometric analysis*

For both male and female *Lybia edmondsoni* a highly significant regression ( $p < 0.01$ ) of propodus length vs. carapace width was found ( $r = 0.909$  and  $0.831$ , respectively). The slope of the regression line for males was not significantly different from that of females (Fig. 2). Male and female crabs in our study were probably sexually mature, since females collected from the field bearing eggs were well within the lowest size range of individuals tested.

#### *Agonistic ethogram of Lybia edmondsoni*

##### *Non-contact acts carried out with anemones*

Twitch (TWT) – A rapid ( $< 1$ sec) and short lateral extension of the propodus of the cheliped, with either left, right, or both chelae moving simultaneously with anemones. The amplitude is approximately 1–3 mm, measured at the distal margin of the propodus. Occasionally, it is accompanied by a similar “jerking” motion by the entire body.

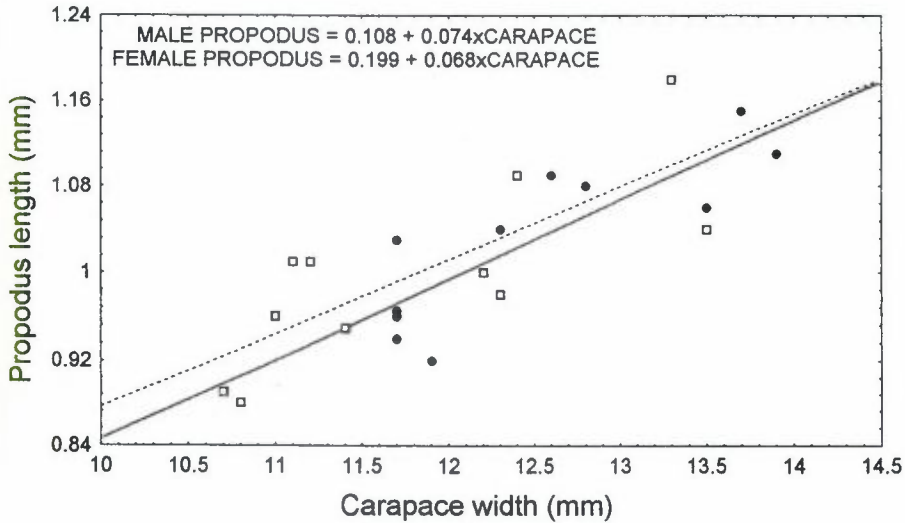


Figure 2. Regression of propodus length vs. carapace width for male (circle, full line) and female (square, dashed line) *Lybia edmondsoni*.

Wave (WVE) – Slow movement of either the left, right, or both chelae in a relatively wide angle in the horizontal axis. Chelae with anemones can either be extended or kept close to anterior carapace.

Extend (EXT) – Extension of left and/or right chelipeds with anemones.

*Contact acts carried out with anemones*

Anemone contact (ACT) – Any contact between a crab's anemone and its opponent.

*Other acts with physical contact between crabs*

Single leg contact (SLC) – A single short contact initiated by one individual where one of its walking leg touches the opponent.

Multiple leg contact (MLC) – Contact initiated by one individual where more than one of its walking legs touches the opponent.

Semi-grapple (SGP) – Multiple contacts of legs initiated by both opponents. Legs are in rapid motion and crabs laterally oriented to each other.

Full grapple (FGP) – Two or more legs of each crab are interlocked, while anemones are extended. Crabs may be oriented to each other in various positions (Fig. 3).

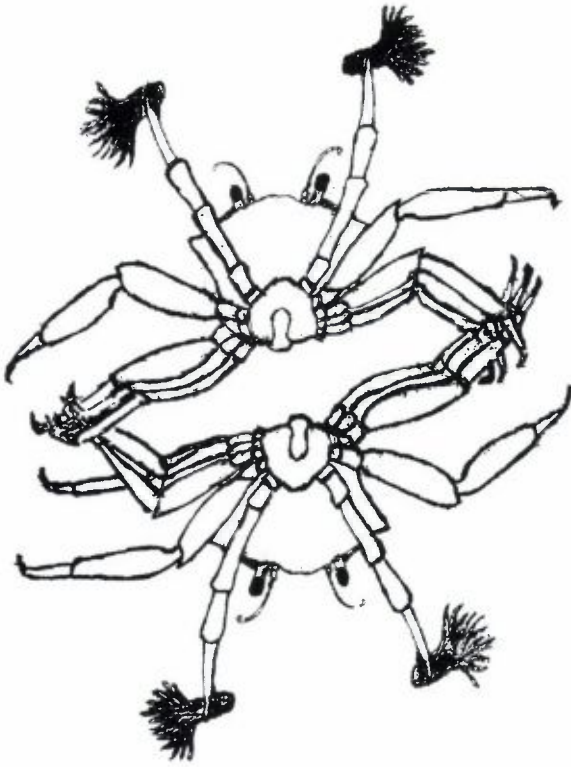


Figure 3. Two fighting *Lybia edmondsoni* in the Full Grapple (FGP) position. Walking legs are interlocked while anemones are extended in opposite directions.

#### *Maintenance activities*

Rub legs (RBL) – One or more legs stroking adjacent legs. Usually involves two legs at a time.

Mouth anemone (MOA) – Contact between basal disk or column of anemone by maxillae and maxillipeds of crab.

#### *Acts increasing or decreasing distance between crabs*

Approach (APR) – A gradual decrease of distance between crabs when they are at most 5 cm apart. A distance of at least 2 carapace widths is covered.

Rush (RSH) – A rapid approach to an opponent, not necessarily closer than 5 cm. During a rush a distance of at least 2 carapace widths is covered.

Lunge (LUN) – A leap or large, rapid incremental movement towards or away from an opponent, not necessarily within a 5 cm distance.



Retreat (RET) – A gradual increase of distance between crabs when they are at most 5 cm apart. A distance of at least 2 carapace widths is covered.

Flee (FLE) – A rapid increase of distance between crabs when they are at most 5 cm apart. A distance of at least 2 carapace widths is covered.

#### *Symmetrical contests in Lybia edmondsoni*

Five parameters of male and female contests (e.g., number of acts and number of bouts per contest) were compared (Table 1), indicating the lack of any significant difference between the sexes (Mann Whitney U test;  $p > 0.05$ ). Both male and female crabs avoided proximity and contact with their adversaries. Crabs spent less than two minutes at a time within 5 cm from their rival (i.e., bout duration). The total time spent in physical contact (combined duration of SLC, MLC, SGP and FGP) was very short, averaging nearly 20 and 60 sec in males and females, respectively.

Table 1. Means and standard deviations of several parameters of intraspecific aggressive encounters calculated separately for males and females of *Lybia edmondsoni*

Sex	No. of acts per contest	Time of physical contact during contests (sec)	No. of bouts per contest	No. of acts per bout	Bout duration (sec)
Male	214.7±130.4	20.7± 11.0	10.5±6.6	9.2±2.0	50.6±29.2
Female	201.5 ± 82.6	61.8±106.5	9.5±5.5	14.3±6.2	105.3±95.5

The frequency of the 15 behavioral acts (see ethogram) recorded, is presented separately for each gender in Fig. 4. Three behaviors carried out with anemones (Twitch, Wave, & Extend) comprised nearly 50% (57.6% for males, and 47.8% for females) of all acts performed by these crabs. In contrast to the very frequent display of anemones at some distance from its adversaries, touching the other crab with its anemone was very rare. This behavior was not observed at all in male contests, and seldom (<1% of total number of acts) in females. Acts which involve physical contact between legs of opponent crabs (SLC, MLC, SGP and FGP) were relatively rare, 5.8% and 7.5% of all male and female acts, respectively. The two maintenance behaviors (RBL and MOA) were frequently displayed by both males and females (Fig. 4). We also observed these acts in both males and females maintained in isolation.



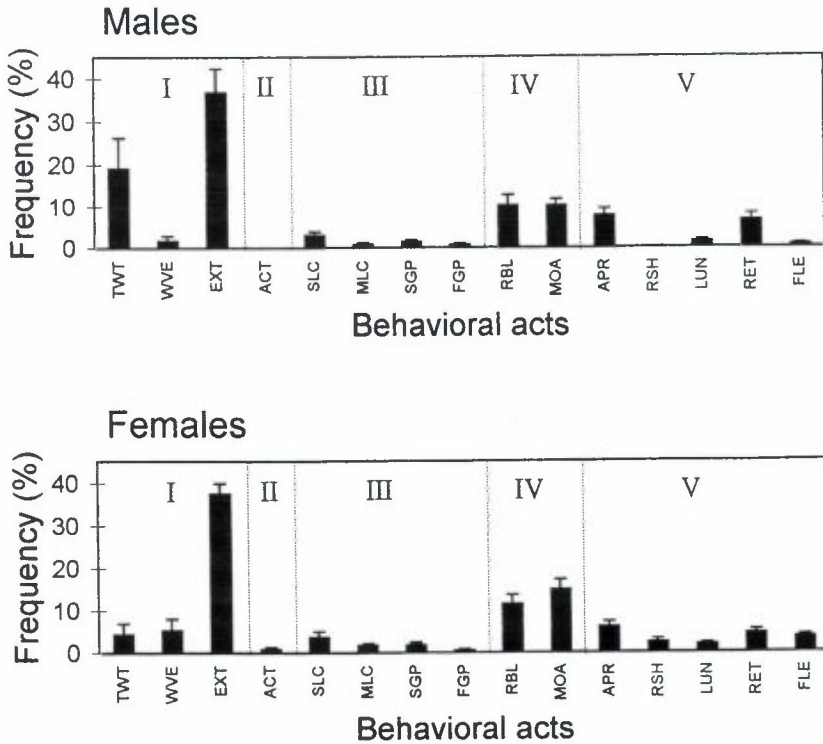


Figure 4. Mean frequency with standard error of 15 different acts during intraspecific aggressive encounters in *Lybia edmondsoni* presented for males and females. I. Non-contact acts carried out with anemones. II. Contact acts carried out with anemones. III. Other acts with physical contact between crabs. IV. Maintenance activities. V. Acts increasing and decreasing distance between crabs (see ethogram for act abbreviations).

The identity of the winner of each contest was established and the motor activity and the frequency of the common acts were contrasted in winners and losers separately for each gender. The pattern of motor activity of males and females was similar (Table 2). However, they differed in motor activity with regard to the effect of winning or losing the contest. In males, losers crossed significantly more lines than winners (Table 2, Wilcoxon matched-pairs signed-ranks test,  $p < 0.03$ ). In females, however, the difference was not significant. The most common behavioral act displayed during contests was "Extend", performed at similar rates by winners and losers of both sexes (Table 2). The act "Wave" appears to be displayed more by losers, however, this relationship was only significant for females (Wilcoxon matched-pairs signed-ranks test;  $p < 0.05$ ). "Twitch", a conspicuous, rapid and short movement of the

chela's propodus, was performed singly, or in repetitive series, consisting at least of two twitches performed within a 5 sec time interval. Series of twitches consisting of  $4.0 \pm 2.5$  acts, were performed at a rate of  $0.6 \pm 0.2$  acts per sec. Males and winners performed this act more often than females and losers, however both these effects were non significant (Table 2).

There were no significant differences in the frequency that the act "Rub Leg" was performed by male and female, winners and losers (Table 2). The act "Mouth Anemone" was performed at similar rates by the two genders, however, male losers performed this act more often than winners (Wilcoxon matched-pairs signed-ranks test,  $p = 0.059$ ).

Table 2. Motor activity and frequency of acts performed per contest (mean  $\pm$  S.D.) by male and female winners and losers in intraspecific symmetrical contests of *Lybia edmondsoni*. Different letters designate significant differences ( $p < 0.05$ ) between winners and losers of the same sex.

Motor activity	Acts carried out with anemones			Maintenance activities	
	EXT	WVE	TWT	RBL	MOA
<b>Males</b>					
Winners					
95.5 $\pm$ 53.3a	35.0 $\pm$ 32.5	0.3 $\pm$ 0.8	14.2 $\pm$ 20.9	7.3 $\pm$ 7.8	11.7 $\pm$ 13.9 b
Losers					
52.7 $\pm$ 36.5b	43.7 $\pm$ 22.0	4.3 $\pm$ 7.4	9.3 $\pm$ 15.5	6.0 $\pm$ 8.9	20.7 $\pm$ 22.6 a
<b>Females</b>					
Winners					
61.3 $\pm$ 59.5	37.0 $\pm$ 20.0	1.2 $\pm$ 1.6 b	11.3 $\pm$ 23.0	14.1 $\pm$ 8.0	16.8 $\pm$ 12.0
Losers					
67.5 $\pm$ 30.5	37.3 $\pm$ 19.8	8.2 $\pm$ 6.2 a	1.0 $\pm$ 1.6	10.6 $\pm$ 8.5	11.0 $\pm$ 7.8

#### *Observations on crabs lacking one or both anemones*

During the course of this study, we observed several unusual phenomena with crabs lacking one or both anemones. In a contest between two crabs that carried no anemones we observed that the chelae were used very similar to chelae of crabs carrying anemones. Even during a particularly intense "Grapple", chelae were held away from the opponent.

We removed one anemone each from two individuals at different times, and collected two individuals with only one anemone. In all cases the crabs were subsequently observed with two incomplete anemones in each chela, in a time

frame of one hour to nine days. In one case, we actually observed a crab in the midst of "splitting" its anemone into two parts by slowly pulling it apart. A tissue thread was clearly seen between the two halves as the crab moved its chelae apart laterally. Each piece of "split" anemone later regenerated giving the crab a complete anemone in each chela.

#### 4. Discussion

##### *Anemone use in intraspecific contests*

Ample evidence was accumulated in this study on the lack of anemone use during close contact. Although the crabs frequently used their anemones in intraspecific interactions during contests (i.e. Twitch, Extend, & Wave), they did so without touching their opponents. Even when extending one claw at close range, crabs invariably did so with the claw furthest away from the opponent. Furthermore, during Full Grapple at very close range, opponents extended their claws in opposite directions, away from each other. Actual contact between anemones and opponents was brief, rare and seemed to occur due to an accidental movement of one of the crabs.

Several hypotheses for the lack of use of anemones as a contact weapon during intraspecific contests are suggested:

1. *Triactis producta* are highly toxic to *Lybia edmondsoni*. Crabs avoid using anemones in intraspecific contests due to their high potential of severely harming both the winner and loser of a fight. According to game theory, the greater the risk of being severely wounded in a fight compared to the benefit, the lower the escalation level (Maynard-Smith and Price, 1973). Fighting without using a dangerous alternative was also reported for poisonous snakes which fight conspecifics without using their venom (Shaw, 1948; Thomas, 1961; Carpenter et al., 1976).

2. *T. producta* are non-toxic to *L. edmondsoni*. Anemones constitute an inefficient weapon and are therefore not used in combat. Schmitt (1965), cited in Guinot (1976) reported that small fish were paralyzed following contact with the tentacles of an anemone held by a *Lybia*. However, our preliminary experiments on sensitivity of *L. edmondsoni* to *T. producta* were inconclusive.

3. *T. producta* are a valuable resource to *L. edmondsoni* and are not used in combat to prevent anemone damage or removal by the opponent. Anemones were almost always held away from opponents. However, it is not known whether the anemone could be damaged by objects in the natural environment (i.e. sand or gravel) during intense acts such as Grapple. We did not observe any exchange of anemones, ritualized or otherwise, between opponents during the contests. In all 12 contests the losers retreated with anemones intact. This phenomenon

may be due to the lack of importance of anemone size or the difficulty in both a ritualized and forceful exchange or removal of anemones. Anemones could be easily damaged if they were pulled from the spines holding them in place in the chelae. A ritualized exchange of four small anemones without losing them (i.e. to water current or other crabs) could be difficult. In contrast, hermit crabs routinely exchange shells during contests (Elwood and Neil, 1992). In this case, however, only two items are switched and these are much larger and damage resistant. Removal of anemones was only observed by one of us (GCF, unpub. obs.) when two small *L. edmondsoni* with anemones were introduced into an aquarium with a large conspecific deprived of anemones.

#### *Male and female fighting behavior*

Our morphological data support our observations on the agonistic behaviors of *L. edmondsoni*. The similarity in the regressions between propodus length and carapace width between males and females indicates that there is no sexual dimorphism for this character which is directly involved in anemone holding. In many decapod crustaceans the claws are more developed in males, probably contributing to differences in fighting behavior between genders (Hyatt, 1983). However, we saw a marked similarity in the fighting behaviors of male and female crabs during contests. This similarity may be due to the fact that the claws of the two genders are similarly specialized for holding anemones, and not for grasping food or adversaries. Despite the overall similarity in fighting behavior, males seemed to avoid close proximity to opponents more than females. Male losers, for example, displayed a higher rate of motor activity in part because of consistent attempts to move away from winners. It could be that males are more territorial than females, or have larger individual space once dominance has been established. Field studies on the distribution of crabs are needed to clarify these points.

#### *The crab-anemone relationship*

The use of anemones in agonistic displays and our other observations support past observations on the importance and complexity of the crab-anemone relationship for *L. edmondsoni*. Mouthing the anemone (MOA) pedal disk and column could fulfill several functions. Duerden (1905) suggested that it served to remove mucus with food from the anemone. Another function may be to temporarily affect anemone structure, particularly the pedal disk. By "masticating" the pedal disk, the crab may alter the shape and ability of disk to adhere to surfaces, making it easier to handle. We did note that captive anemones had nearly cone-shape pedal disks. It is also possible that mouthing



the anemone allows *L. edmondsoni* to increase turgor pressure in the tentacles, making the anemone an even more impressive weapon. A fourth explanation is that crabs mouth the anemone to readjust their grip on the actinians. In this way, a crab could loosen its grip with the claw without dropping the anemone entirely.

Anemones are crucial for *L. edmondsoni* survival, as revealed from the fact that no crabs without anemones were collected by us. This finding corroborates with most early reports (Duerden, 1905), with the exception of that of Borradaile (1902) who reported collecting some *L. tessellata* without anemones. In our study *L. edmondsoni* specimens, molted at night. When examined in the following morning they were already holding their anemones in their claws, despite their still soft exoskeleton. However, the two crabs which had anemones removed for a pilot contest survived well in captivity several months. Under those conditions food was presented daily, ad libitum. In the field a crab without anemones suffers from two disadvantages: lack of protection from predators and lack of an efficient means of collecting food (Duerden, 1905).

The crab/anemone symbiosis has affected both the morphology and behavior of *L. edmondsoni*. The morphological adaptations of *Lybia* for holding anemones, particularly the size and structure of chelae and the great mobility of the propodal-carpal joint, have been described in detail (Duerden, 1905; Guinot, 1976). In the present study, we found that the partnership also affected the agonistic behavior of the crab. The chelae of *L. edmondsoni*, specialized for holding anemones, were not used to grasp other objects or opponents during contests, even when the crabs were deprived of anemones. Contacts between legs during agonistic interactions (Single Leg Contact, Multiple Leg Contact, Semi-Grapple, and Full Grapple) seemed to have replaced the usual ritualized intertwining of the chelae reported in several other brachyurans (Schone, 1968; Warner, 1970; Lindberg, 1980) and forcefully grasping (Huber, 1987). Three commonly used acts (Extend, Wave, and Twitch) were carried out with the anemones during contests. *L. edmondsoni* refrained consistently from using anemones, but displayed its "weapons" from a distance. As a result, its fighting behavior is more ritualized, with minimal contacts between opponents.

So far, little knowledge is available on the effect of crab/anemone partnership on the anemone. Duerden (1905) suggested that advantages for the anemone include reaching new sources of food and being supplied with extra oxygen due to the crab movements, while disadvantages might include being robbed of its food by the crab. In our study, we observed two other effects on the anemone induced by the crab. The first was the suggested change in pedal disk structure as a result of mouthing. Other structural changes between carried and free-living *T. producta* were described by Cutress (1977). The second effect we

observed was *L. edmondsoni* forcing asexual reproduction upon anemones by splitting them. More studies are needed on reproduction and growth of free-living and associated anemones in order to characterize the relationship fully.

### Acknowledgements

Many thanks are due to Profs. E.S. Reese and G. Losey for welcoming the first author into their laboratories, and for constant advice and encouragement throughout that period. We are especially grateful for the assistance of Daniel Karplus for his help with data entry, word processing, and video tape editing. We also offer a big "Mahalo" to the staff of the Hawaii Institute of Marine Biology, Kaneohe, for their help and hospitality. We wish to thank Dr. A. Barki for his valuable comments on the manuscript.

### REFERENCES

- Borradaile, L.A. 1902. Marine Crustaceans. III. The Xanthidae and some other crab. In: *The Fauna and Geography of the Maldives and Laccadive Archipelagos*, vol. 1, Part 3, pp. 237-271.
- Carpenter, C.C., Gillingham, J.C., and Murphy, J.B. 1976. The combat ritual of the rock rattlesnake *Crotalus cepidus*. *Copeia* pp. 764-780.
- Cummins, D.R., Chen, D., and Goldsmith, T.H. 1984. Spectral sensitivity of the spiny lobster, *Panulirus argus*. *Biological Bulletin* 166: 269-276.
- Cutress, C.E. 1977. "Order Corallimorpharia". In: *Reef and Shore Fauna of Hawaii*, Section 1: Protozoa through Ctenophora, D. Devaney, and L. Eldredge, eds. Bishop Museum Special Publication 64:131-147.
- Dales, R.P. 1966. Symbiosis in marine organisms. In: *Symbiosis*. S.M. Henry, ed. Vol. 1, Academic Press, New York, pp. 299-326.
- Duerden, J.E. 1905. On the habits and reactions of crabs bearing actinians in their claws. *Proceedings of the Zoological Society of London* 2: 494-511.
- Elwood, R.W. and Neil, S.J. 1992. *Assessments and Decisions: A study of Information Gathering by Hermit Crabs*. Chapman & Hall, London. 192 pp.
- Goldsmith, T.H. and Fernandez, H.R. 1968. Comparative studies of crustacean spectral sensitivity. *Zeitschrift für Vergleichende Physiologie* 60: 156-175.
- Guinot, D. 1976. La superfamille des Bellioidae et trois sous-familles de Xanthidae (Polydectinae Dana, Trichiinae de Haan, Actaeinae Alcock): Constitution de quelques groupes naturels chez les Crustacés Décapodes Brachyours, I. *Memoirs du Museum national d'Histoire naturelle (Paris), new series A (zoology)* 97: 1-308, Figs. 1-47, pls. 1-19.
- Huber, M.E. 1987. Aggressive behavior of *Trapezia intermedia* Miers and *T. digitalis* Latreille (Brachyura:Xanthidae). *Journal of Crustacean Biology* 7: 238-248.

- Hyatt, G.W. 1983. Qualitative and quantitative dimensions of crustacean aggression. In: *Studies in Adaptation. The Behavior of Higher Crustacea*. S. Rebach and D.W. Dunham, eds. John Wiley & Sons, pp. 113-139.
- Latreille, P.A. 1812. Crustaces et Insectes. In: *Voyage pittoresque a l'Ile-de-France, au Cap de Bonne-Esperance et l'Ile de Teneriffe*, J. Milbert, ed. t. 2. Paris, Le Normant. Crustaces, pp. 270-280.
- Lindberg, W.J. 1980. Behavior of the Oregon mud crab, *Hemigrapsus oregonensis* (Dana) (Brachyura, Grapsidae). *Crustaceana* 39: 263-281.
- Maynard Smith, J. and Price, G.R. 1973. The logic of animal conflict. *Nature* 246: 15-18.
- Richter, F. 1880. Decapoda. In: *Beiträge zur Meeresfauna der Insel Mauritius und der Seychelles*. Moebius, K., ed. Berlin, pp. 137-178, Tables 15-18.
- Ross, D.M. 1974. Behavior patterns in associations and interactions with other animals. In: *Coelenterate Biology: Reviews and New Perspectives*. L. Muscantine and H.M. Lenhoff, eds. Academic Press, New York. pp. 281-312.
- Ross, D.M. 1983. Symbiotic relations. In: *The Biology of Crustacea*. Vol 7. F.J. Vernberg and W.B. Vernberg, eds. Academic Press, New York, pp. 163-200.
- Sakai, T. 1961. New species of Japanese crabs from the collection of His Majesty the Emperor of Japan. *Crustaceana* 3: 131-150.
- Schone, H. 1968. Agonistic and sexual display in aquatic and semi-terrestrial brachyuran crabs. *American Zoologist* 8: 641-654.
- Shaw, C.E. 1948. The male combat "dance" of some crotalid snakes. *Herpetologica* 4: 137-145.
- Takeda, M. and Miyake, S. 1970. *Lybia edmondsoni* sp. nov., a new anemone crab from the Hawaiian Islands. *Proceedings of the Japan Society of Systematic Zoology* 6: 11-15.
- Tan, C.G.S. and Ng, P.K.L. 1994. A new species of anemone-carrying crab from New Caledonia (Decapoda: Brachyura: Xanthidae: Polydectinae). *Proceedings of the Biological Society of Washington* 107: 738-742.
- Thomas, E. 1961. Fortpflanzungskämpfe bei Sandottern (*Vipera ammodytes*). *Zoologischer Anzeiger*. Supplement 24: 502-505.
- Ward, M. 1933. New genera and species of Marine Decapoda, Brachyura from the coasts of New South Wales and Queensland. *Australian Zoologist* 7: 377-394.
- Warner, G.F. 1970. Behavior of two species of grapsid crab during intraspecific encounters. *Behaviour* 36: 9-19.