

INTRASPECIFIC COMPETITION, STEALING AND PLACEMENT OF THE SYMBIOTIC SEA ANEMONE *CALLIACTIS TRICOLOR* BY THE HERMIT CRAB *DARDANUS PEDUNCULATUS*

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Abstract. The hermit crab *Dardanus pedunculatus* and the sea anemone *Calliactis tricolor* engage in a mutualistic relationship in the tropical reef ecosystem of Mo'orea, French Polynesia. This mutualism is shaped by the pressures on *D. pedunculatus* individuals to acquire actively and compete for *C. tricolor* in the wild. *D. pedunculatus* exhibits a consistent trend in behavior when competing for and placing *C. tricolor* on its gastropod shell. Since *C. tricolor* seems to be a valuable resource to *D. pedunculatus*, this species engages in intraspecific competition. Experiments were designed to examine the behaviors of *D. pedunculatus* under laboratory conditions when competing for and placing their symbiont. *D. pedunculatus* individuals steal *C. tricolor* from one another, with larger *D. pedunculatus* dominating in these encounters. In contests between two *D. pedunculatus* individuals, competition is also based on size dominance. The size of the cheliped of the left-handed *D. pedunculatus* is the most strongly correlated to winning a fight for *C. tricolor*. The placement of *C. tricolor* follows a distinctive symmetrical pattern on the shell of *D. pedunculatus*. By equally distributing *C. tricolor*, *D. pedunculatus* could possibly be protecting itself from attack coming at any angle. These behaviors stem from the benefits that both organisms derive from their union. Understanding the behavioral patterns linked to this symbiotic relationship helps to examine the broader web of interactions that build the complexity of reef ecosystems.

Key words: *Mo'orea; French Polynesia; hermit crab; Dardanus pedunculatus; sea anemone; Calliactis tricolor; mutualism; intraspecific competition; placement; behavior.*

INTRODUCTION

The expanse of symbioses in tropical marine environments offers insight on the intricate relationships that shape the delicate ecosystem of a coral reef (Hay 2004). In a symbiotic relationship, two different organisms live in a prolonged physical association (Boucher et al. 1982). A mutualism is a kind of symbiosis where two organisms derive a benefit from their association (Boucher et al. 1982). Mutualistic relationships have been associated with behavior patterns ingrained in each organism (Hay 2004). Symbioses involving sea anemones occur throughout many different tropical marine environments such as the one found in Mo'orea, French Polynesia. A classic example of such a symbiosis is the association between the sea anemone *Heteractis magnifica* and the fish *Dascyllus trimaculatus*. The juvenile fish gains protection from predators with the anemone's stinging tentacles while it eats the parasites off the anemone and keeps it healthy (Schmitt 2003). The stinging nematocysts of sea anemones are also an advantage for certain crabs, such as the anemone-wielding crab *Lybia edmondsoni* that wards off opponents by holding the anemone *Triactis protucta* in its claws (Karplus 1998). Sea anemones are also found living symbiotically on shells of different species of hermit crabs in many warm and tropical seas ranging from the Pacific Ocean to the Mediterranean Sea (Ross 1960). The association of hermit crabs and anemones is so widespread that it has evolved at least twice independently (Gusmao 2010). I studied the hermit crab *Dardanus pedunculatus* that is symbiotic with the anemone *Calliactis tricolor* and its behavior towards its symbiotic anemone with the goal of contributing to the knowledge of a successful type of symbiosis that exists in many tropical coral reef ecosystems.

The mutualistic association between the hermit crab *D. pedunculatus* and the sea anemone *C. tricolor* resembles that of other hermit crabs symbiotic with anemones. The hermit crab gains protection from predators due to the excretion of acontia, long filamentous stinging nematocysts, by the anemone (Brooks 1993). The stinging tentacles of the anemone also contribute to repelling predators such as *Octopus* sp. (Ross 1971). The anemone, in turn, gains facilitated nutrition from

the messy feeding of the hermit crab (Brooks 1993). *D. pedunculatus* and *C. tricolor* seem to derive similar benefits from their relationship. Although the association of hermit crabs and anemones has usually been found to be mutualistic (Brooks 1993), recent research brought to light the possible predation of *D. pedunculatus* on *C. tricolor* in a situation of starvation (Imafuku 2000). The close relationship of hermit crabs and anemones has been researched to better understand how this kind of mutualism is established and long-lived.

D. pedunculatus displays similar behavior patterns towards *C. tricolor* as the ones described for other species of hermit crabs towards their symbiotic sea anemone. Many species of hermit crabs symbiotic with sea anemones have been found to engage in specialized behaviors towards their symbiont (Cutress 1969, Ross 1979). The detachment of anemones is a consistent behavior displayed by the hermit crabs (Ross 1961, Ross 1968, Ross 1970). The crabs relax the pedal disk of the anemone using their cheliped and appendages (Ross 1968) to then place the anemone on their shell, although completion of the attachment is done by the anemone (Ross 1968, Ross 1970). The anemone seems to represent a valuable resource to the hermit crab since it actively acquires it in a similar way to how it gets the gastropod shell it lives in (Abrams 1987, Vafeiadou 2011). Gastropod shells are a resource often fought over by hermit crabs (Arnott 2007). It has been found by Ross (1979) that interspecific competition for anemones is present amongst certain populations of hermit crabs. However, the behavioral patterns of *D. pedunculatus* individuals competing for their symbiont have not been examined. I studied the intraspecific competition between *D. pedunculatus* individuals for *C. tricolor* to progress towards the better understanding of their relationship in the wild.

The relationship between hermit crab and anemones in the wild seems to be steady since the placement of the anemones on the gastropod shells of different species of hermit crabs has been observed to follow a pattern (Brooks 1989). Since the hermit crab is mostly responsible for bringing the anemone in contact with its shell, it has control over where the anemones get placed even though the anemones are minimally able to move on their own (Brooks 1995). The placement and number of the sea anemones on the shell of the hermit crab have been found to correlate positively with survival of a predator attack, with anemones closest to the aperture of the shell being associated with the most security (Brooks 1989). Although the anemones increase the weight carried by the hermit crab and could hamper their overall mobility, the greater the number of them present on a shell increases the likelihood of their survival of an *Octopus sp.* attack (Brooks 1988). The question of whether hermit crabs place the anemones in a symmetrical and weight balanced manner on their shell has been studied experimentally for the hermit crab species *Pagurus pollicaris* but never for *D. pedunculatus* (Brooks 1989). I hypothesize that the placement and number of *C. tricolor* added to the shell follows a specific symmetrical pattern.

To increase its protection from predators, *D. pedunculatus* developed an association with *C. tricolor* to which a set of behaviors is attached. The way *C. tricolor* is placed onto the shell by *D. pedunculatus* appears to be organized in a similar manner than anemones placed by other species of hermit crabs. I hypothesize that *D. pedunculatus* places *C. tricolor* following a distinctive symmetrical pattern. The presence of *C. tricolor* as another resource to acquire influences the competition between *D. pedunculatus* individuals. I hypothesize that intraspecific competition involving *D. pedunculatus* will be prevalent in the form of aggressive behaviors. Since stealing of anemones has been observed between three species of hermit crabs (Ross 1979), I hypothesize that *D. pedunculatus* will steal *C. tricolor* from other individuals intraspecifically. Under experimental conditions, my hypotheses is that *D. pedunculatus* individuals with a size advantage will dominate others in intraspecific competitions for *C. tricolor*. By studying the competition for and placement of *C. tricolor*, this study aims to define more clearly the behavioral repertoire of *D. pedunculatus* towards its symbiont.

METHODS

Study site

Dardanus pedunculatus individuals were observed and collected at two different sites during night snorkeling in Mo'orea, French Polynesia. The first site was located at the University of California, Berkeley Gump Research Station (17°29'23.10"S, 149°49'31.78"W) and the second at the public beach of Temae (17°29'53.58"S, 149°45'40.46"W). Both sites were chosen out of convenience and shallow depths that made collection of *D. pedunculatus* possible with snorkeling. The sites

were composed of a mixture of sand, coral reef and coral rubble at depths ranging between 0.3m and 4m. The research station site contained more sedimentation and less live coral than the public beach where a larger and more developed reef is found. The water temperature at the two sites averaged 28°C.

Preliminary observations and collection

Each *D. pedunculatus* encountered during night snorkeling was observed for twenty minutes with a dive lamp. During field observations, a record was kept that included information about the substrate the crab was found on, time of observation, interactions with other organisms and behavior it was engaging in before collection. In thirteen independent sessions of night snorkeling between September 29th, 2011 and November 18th, 2011, a total of 51 *D. pedunculatus* were collected, placed in individual plastic containers with seawater, and brought to the laboratory within an hour after collection. *D. pedunculatus* individuals were acclimated in individual open-circulating seawater aquariums at the University of California Berkeley research station for 24 hours. The seawater in the aquariums came directly from Cook's Bay. They were fed daily with live krill and plankton collected at night with a plankton net and dive lamp.

After the acclimation period was over, observations of *D. pedunculatus* individuals were recorded in the wet lab before any manipulations began. *D. pedunculatus* were photographed from three different angles: from above, along its side and from below. The width of the shell was recorded along its longest diameter at the aperture. Cheliped size was measured and used as an indicator of body size in the future experiments. The number, size and position of *C. tricolor* on the shell of *D. pedunculatus* were recorded. To measure *C. tricolor* size, the longest diameter across the pedal disk was measured. Each *D. pedunculatus* was assigned a number to keep track of during experiments and was identified by its size, type of gastropod shell it inhabited and any particular markings present on its shell. No more than six specimens were ever collected in one night. Every tank used for experiments contained sand and coral rubble.

A placement code was established from preliminary observations to record how the *C. tricolor* were positioned on the shell (Figure 1). The shell was divided into three equal sized columns, with the middle column further divided into three rows. This placement code was also used to record the results of experiments. Data about both types of anemones present on the top and on the bottom around the shell's aperture were recorded. Although only *C. tricolor* was examined in this study, *D. pedunculatus* individuals also carried small white anemone (*Sagartiomorpha paguri*) around the aperture of their shell.

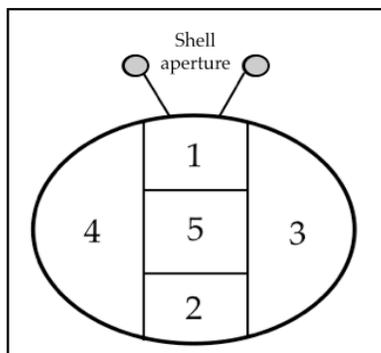


FIG. 1. The placement code that was used to record how *C. tricolor* was distributed on the gastropod shell. This is a dorsal view of the shell.

Anemone removal

The first manipulation was the removal of *C. tricolor* from the shells of *D. pedunculatus*. They were removed gently using a thin flat metal plate slid under the rim of the pedal disk. Once removed, the *C. tricolor* were left to settle in their own aquarium (30x20x20cm). They were left to acclimate to their new substrate for two hours before experiments began.

a) Intraspecific competition: stealing

To examine the stealing behavior of *D. pedunculatus*, two specimens were placed in the same tank for twelve hours. One *D. pedunculatus* had all *C. tricolor* removed, and the other had all *C. tricolor* removed except for one remaining on its shell. After the time elapsed, stealing was recorded if the *C. tricolor* was found on the other *D. pedunculatus*. The placement of the stolen *C. tricolor* was also recorded. The experiment was repeated using different pairs of *D. pedunculatus*, without running more than two trials with one specimen. There were 34 trials conducted. The smaller *D. pedunculatus* was left with the *C. tricolor* on its shell at the beginning of 22 trials, and the larger one was left with it in 12 trials.

The difference of cheliped size was used to calculate the size difference between *D. pedunculatus* individuals. Size difference within stealing trials was measured by subtracting the cheliped size of the *D. pedunculatus* without a *C. tricolor* on its shell from the cheliped size of the *D. pedunculatus* with one at the beginning of the experiment. A negative cheliped size difference thus meant that the smaller *D. pedunculatus* of the pair had the *C. tricolor*. The stealing behavior was videotaped outside of the glass pane of the aquarium with the two *D. pedunculatus*.

For statistical analysis, a Pearson's Chi-square test was used to test the significance of stealing events. The stealing behavior was defined as the sequence of events defined in Appendix A (Fig A).

b) Intraspecific competition: contests

Contests were setup to examine how *D. pedunculatus* individuals interact when competing for one *C. tricolor*. Two specimens with all their anemones removed from their shell were placed at equal distances from a *C. tricolor* attached to a piece of coral rubble in a tank. The cheliped size difference, as well as the shell size difference was recorded. The two *D. pedunculatus* were observed for 30 minutes, and then the experiment was left to run for twelve hours overnight. In the morning, the location and size of *C. tricolor* was recorded if it was attached to one of the *D. pedunculatus*. There were 33 trials conducted. A single trial resulted in no attachment of *C. tricolor* to either *D. pedunculatus* and was excluded from statistical analysis.

For statistical analysis, both cheliped and shell size were examined independently as possible causes for winning a contest. Then, the two measurements were joined using principle component analysis to create a new size factor. A Pearson's chi-square test was used to analyze the winners of the contests for each size component. The chance of winning was expected to be 50% for each *D. pedunculatus* if the null hypothesis was supported.

c) Placement of *C. tricolor*

In order to study placement preference, *D. pedunculatus* specimens with all *C. tricolor* removed were placed individually in a tank along with differently sized *C. tricolor* attached to coral rubble pieces. Small *D. pedunculatus*, of cheliped size below two centimeters, were presented three *C. tricolor* and the larger ones, of cheliped size larger than two centimeters, were presented six *C. tricolor*. The difference in number of *C. tricolor* was due to the limited number of them extracted from the shells of the specimens collected. The experiment ran for twelve hours overnight. The next day, the number and placement of *C. tricolor* on the shell of *D. pedunculatus* was recorded. To study the presence or absence of symmetry in the placement of *C. tricolor*, the presence of a mirror image of *C. tricolor* distribution on the shell was recorded. One trial was done for every *D. pedunculatus* individual. There were 28 trials conducted. A total of 108 *C. tricolor* were studied in the 28 experimental trials, and 152 *C. tricolor* were studied in preliminary observations of the placement prior to manipulations. In the experiments, 84 of the 108 *C. tricolor* presented were added onto the shells of *D. pedunculatus* with their placement recorded.

Both the results from placement experiments and from preliminary observations were used to examine how *C. tricolor* was placed by *D. pedunculatus*. It was assumed that *C. tricolor* movement after their attachment on the shell was negligible. The placement of the single *C. tricolor* at the end of both the stealing and fight experiments was also used to see if a placement pattern emerged.

For statistical analysis, the average number of anemones placed in each zone on the shell

was used to find a possible pattern in the placement of *C. tricolor*. One-way ANOVA tests were used for both experimental and observational placement tests to analyze the average number of *C. tricolor* placed in each zone of the shell. It was expected that each column on the shell would carry an equal number of *C. tricolor* if they were placed with symmetry and equal distribution. A Pearson's Chi-square test was employed to examine the similarity of *C. tricolor* distribution between the three columns. To examine the similarities between average number of *C. tricolor* in the zones on the shell, a Tukey-Kramer test was employed.

Release

The *D. pedunculatus* specimens were kept a maximum of seven nights in the laboratory. For their last night in the tank, *D. pedunculatus* were left overnight with the same number of *C. tricolor* they originally had on their shells in order for them to restore their original number before being released in the wild. They were always freed at night.

RESULTS

a) Intraspecific competition: stealing

D. pedunculatus stole *C. tricolor* from other individuals. Larger *D. pedunculatus* specimens stole from smaller ones (Chi-square, $\chi^2=18$, DF=1, $p<.0001^*$). The larger *D. pedunculatus* stole in 82% of the experiments where the smaller one had the *C. tricolor* on its shell. In the 22 trials where the smaller *D. pedunculatus* carried a *C. tricolor*, 18 resulted in stealing by the larger specimen. The smaller *D. pedunculatus* never stole from the larger one in the 12 trials where the larger *D. pedunculatus* carried a *C. tricolor*. Stealing of *C. tricolor* occurred at various cheliped size differences between the *D. pedunculatus* (Fig. 2).

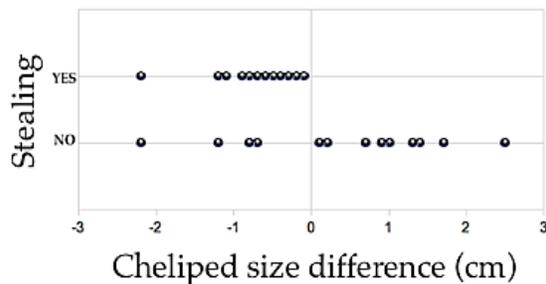


FIG. 2. Stealing of *C. tricolor* based on the difference of cheliped size between the two *D. pedunculatus* individuals. A negative cheliped size difference represents the scenario where the smaller crab had the anemone at the beginning of the experiment. (n=32)

b) Intraspecific competition: contests

Cheliped and shell size were factors that influenced winning contests for *C. tricolor*. The *D. pedunculatus* individual with the larger cheliped of the pair obtained the *C. tricolor* in the majority of cases at the end of the overnight contests (Table 3) (Chi-square, $\chi^2=25$, DF=1, $p<.0001^*$). Shell size was also a determining factor in winning the contests (Table 3) (Chi-square, $\chi^2=6$, DF=1,

p<.01*).

Cheliped and shell size correlated positively (Fig. 4) (linear regression, $R^2=0.39$, $p<.0001^*$). They were combined into a new size factor using principle component analysis which was used to calculate a new size difference between the pair of *D. pedunculatus* (PCA, $p<.0001^*$). I used the first principle component, which summarizes 81.8% of the variation in the shell and cheliped sizes. The *D. pedunculatus* with the larger size factor of the pair won the majority of contests (Table 3) (Chi-square, $\chi^2=21$, $DF=1$, $p<.0001$).

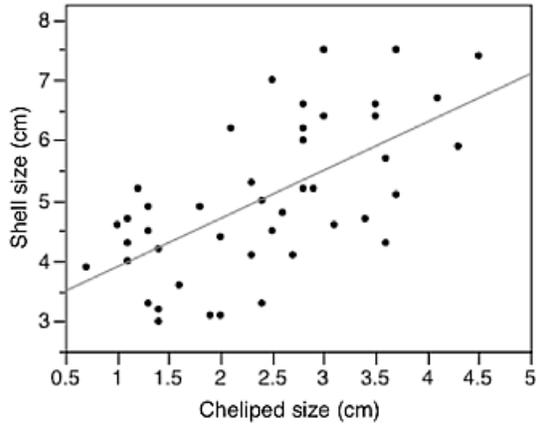


FIG. 4. Positive correlation between cheliped and shell size of *D. pedunculatus* with adjusted linear fit line. *D. pedunculatus* with large chelipeds tend to have a large shell size (linear regression $R^2=0.39$, $p<.0001^*$).

TABLE 3. Cheliped and shell size as factors of winning overnight contests of two *D. pedunculatus* individuals for one *C. tricolor*.

	Larger won	Smaller won	Total
Cheliped	30*	2	32
Shell	23*	9	32
Size Factor	29*	3	32

Notes: The size factor refers to a combination of both cheliped and shell size using principle component analysis. Each element was a strong determinant of winning the contests. Cheliped size ($\chi^2=25$, $DF=1$, $p<.0001^*$); shell size ($\chi^2=6$, $DF=1$, $p<.01^*$); size factor ($\chi^2=21$, $DF=1$, $p<.0001$).

c) Placement of *C. tricolor*

Placement prior to manipulation

D. pedunculatus individuals displayed *C. tricolor* on their shells in a well-established arrangement prior to manipulations (Fig. 5) (One-way ANOVA, $F_{4,251}=66$, $p<0.0001^*$). The *C. tricolor* were placed evenly on the shell, without any significant difference of distribution between each column (Chi-square, $\chi^2=0.18$, $DF=2$, $p<0.92$). Placements 3 and 4, the right and left sides of the shell, had the most *C. tricolor* placed onto them and were significantly different from each row of placements along the middle column of the shell (Tukey-Kramer, $p<0.0001^*$). Placements 3 and 4 each contained 34% of all the *C. tricolor* on the 51 *D. pedunculatus*. The middle column contained 32% of all *C. tricolor*, with zones 1, 5 and 2 respectively carrying 13%, 5% and 14%.

Symmetry was prevalent in the manner the *C. tricolor* were arranged on the shell (Chi-square, $\chi^2=71$, $DF=1$, $p<0.001^*$). *C. tricolor* was placed in a symmetrical way on 92% of the *D. pedunculatus* studied. The repartition of *C. tricolor* on the un-manipulated *D. pedunculatus* significantly followed a pattern similar to the one found in the experimental conditions.

Placement under experimental conditions

D. pedunculatus individuals followed a distinct placement pattern when setting *C. tricolor* onto their shell under experimental conditions (Fig. 5) (One-way ANOVA, $F_{4,135}=13$, $p<0.0001^*$). The repartition of *C. tricolor* in each column of the shell was even, with no differences between the average number of *C. tricolor* placed in each zone (Chi-square, $\chi^2=0.42$, $DF=2$, $p<0.82$).

D. pedunculatus favored placements 3 and 4 the most, with 31 and 32% respectively of all *C. tricolor* found in these zones (Tukey-Kramer, $p<0.0001$). The proportion of *C. tricolor* in the middle column of the shell summed to 37% of all placed anemones. Individually, placement 1, 5 and 2 contained 12%, 11% and 14% of all the *C. tricolor*.

C. tricolor were placed in a symmetrical manner by *D. pedunculatus* (Chi-square, $\chi^2=52$, $DF=1$, $p<0.0001^*$). In 86% of the trials, *D. pedunculatus* positioned *C. tricolor* with symmetry onto its shell.

Not all *C. tricolor* were added by each *D. pedunculatus* under experimental conditions. *D. pedunculatus* added every presented *C. tricolor* in 54% of the trials.

Other placement recordings

After a single *C. tricolor* was stolen or acquired during a contest experiment, *D. pedunculatus* favored the left and right sides of its shell to place it (Table 6). The percentage of *C. tricolor* placed at the end of these experiments was highest in placements 3 and 4. At the end of stealing occurrences, placements 3 and 4 were highly favored over all other placements (Chi-square, $\chi^2=145$, DF=4, $p<.0001^*$). 3 and 4 were the two main placements preferred by the *D. pedunculatus* that won an overnight contest ($\chi^2=136$, DF=4, $p<0.001^*$).

TABLE 6. Percentages of *C. tricolor* added in the different placements at the end of the stealing events and overnight contest experiments. The placements followed a nonrandom distribution. Stealing: ($\chi^2=145$, DF=4, $p<.0001^*$); Contests: ($\chi^2=136$, DF=4, $p<.0001^*$).

Placement	Stealing Experiment	Contest experiment
	% <i>C. tricolor</i> added	% <i>C. tricolor</i> added
1	0	0
2	1	0
3	49	47
4	50	50
5	0	3

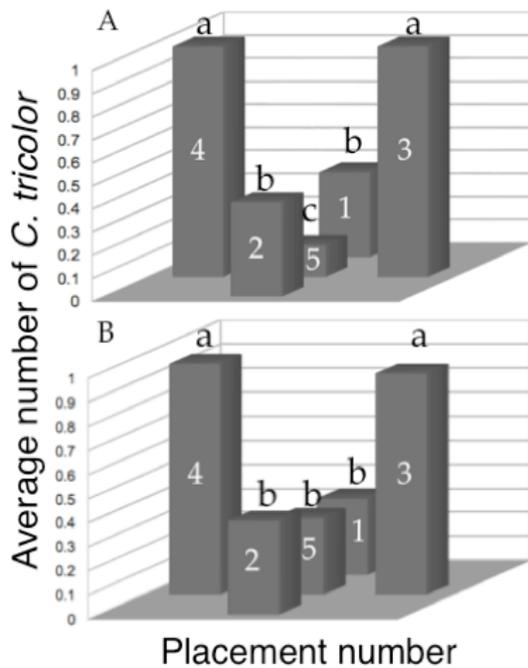


FIG 5. Average number of *C. tricolor* placed by one *D. pedunculatus* in each placement zone of the gastropod shell: prior to manipulation (A) and after placement experiments (B). The numbers in each column refer to a placement zone as established in the placement code (Fig. 1). A pattern emerged in which the dispersion of *C. tricolor* on the shell was nonrandom on un-manipulated *D.*

DISCUSSION

The reported results bring up four points for discussion: (a) the intraspecific stealing behavior by *D. pedunculatus*; (b) size dominance in competitions between *D. pedunculatus* individuals for their symbiotic sea anemone *C. tricolor*; (c) the placement pattern of *C. tricolor* exhibited by *D. pedunculatus*; and (d) how these findings could possibly be applied to *D. pedunculatus* populations in the wild to form a clearer vision of their interactions and the role *C. tricolor* plays as a limited resource.

a) Intraspecific competition: stealing

Intraspecific stealing of *C. tricolor* between *D. pedunculatus* individuals was a consistent behavior displayed by crabs of various sizes. Even when the cheliped of *D. pedunculatus* was only bigger by a few millimeters, dominance was clear and stealing of *C. tricolor* from the smaller crab occurred (Appendix A).

These findings do not agree with a previous study on intraspecific competition that did not find a clear stealing pattern within populations of other hermit crabs *Dardanus arrosor* and *Pagurus oculatus* (Ross 1979). Although these species did not display the stealing behavior in intraspecific encounters, they were found to steal *Calliactis sp.* from other hermit crab species (Ross 1979). Stealing of *Calliactis sp.* was shown to be a part of interspecific competition for the two species studied, but was not found intraspecifically. In my study, however, intraspecific stealing of *C. tricolor* was consistently displayed under the experimental conditions. This suggests that aggression between hermit crabs of the same species could be as important as interspecific competition.

The presence of stealing between the *D. pedunculatus* individuals could suggest that *C. tricolor* is a limited resource in the wild that creates an environmental pressure on *D. pedunculatus* populations. It may be speculated that the limited number of *C. tricolor* in the wild could have shaped the competitive behavior expressed by *D. pedunculatus*. It is implied that *D. pedunculatus* individuals encounter one another often in the wild. If the limited amount of *C. tricolor* in the wild is comparable to the number of gastropod shells available, competition between individuals for their symbiont could be similar to competition for a new shell (Abrams 1980, Abrams 1987). Competition for a resource that improves the hermit crab's fitness is largely found to be size based (Abrams 1987, Hazlett 1981).

b) Intraspecific competition: contests

Even though the two *D. pedunculatus* individuals in each contest had an equal chance to attach the single *C. tricolor* in the aquarium, larger crabs were most likely to win. The competition between *D. pedunculatus* for their symbiotic sea anemone seems to be size based just like competition between other species of hermit crabs for a new gastropod shell to inhabit (Abrams 1980). Competition for a new shell is such a benefit that various hermit crab species compete as to force another hermit crab out of its shell to take it over (Bach 1976). Hermit crabs are known for their aggressiveness (Hazlett 1978) and competition for the same resource is when their temperament is the most obvious (Hazlett 1981).

The added pressure of obtaining symbionts may be a factor that increases competition between *D. pedunculatus* individuals. Although *D. pedunculatus* must change shells as they outgrow them and are sometimes forced to compete for a new habitation with other hermit crabs, they also have *C. tricolor* to compete for in the wild. *C. tricolor* represents a resource to *D. pedunculatus* and fights escalate in a similar manner than for a valuable resource such as a shell in good condition (Arnott 2007). Not only do hermit crabs engage in aggressive behavior towards each other to change shells (Abrams 1980), but some species also exhibit aggression to compete for anemones (Ross 1979). In my study, competition of *D. pedunculatus* surrounding acquiring *C. tricolor* supports previous observations that hermit crabs symbiotic with sea anemones display aggressive behavior to obtain their symbiont when it is found in small concentrations in laboratory conditions (Ross 1979).

The size of the cheliped and shell of *D. pedunculatus* were the main factors that established size dominance in overnight contests for *C. tricolor*. Individuals that had the size advantage dominated the smaller *D. pedunculatus* and attached the anemone to their shell. Cheliped size was the most important factor in establishing dominance in competitive interactions, just like it has been found to be in studies on other species of hermit crabs (Yasuda 2011, Yoshino 2011). The size of the gastropod shell inhabited by *D. pedunculatus* correlated to cheliped size, and when both were clumped to create a new size factor it was also a factor in establishing dominance in the intraspecific competition.

c) Placement of *C. tricolor*

D. pedunculatus placed *C. tricolor* in a nonrandom fashion on its shell. The anemones were placed following a consistent pattern similar to those explained in previous studies (Brooks 1989) where the anemones were placed in a symmetrical distribution on the shell. Although all the *D. pedunculatus* individuals studied lived in different gastropod shells of different species, they placed *C. tricolor* evenly over their shell indicating a preference for symmetry. Even though weight distribution of the anemones was not examined in this study, the symmetrical placement could be a way to balance the weight of the anemones to reduce disturbance of the hermit crab's mobility (Brooks 1988, Brooks 1989). Additionally, *D. pedunculatus* could also be instinctively trying to cover all the different areas a predator could attack in order to maximize the contact with the anemone's stinging nematocysts (Brooks 1988).

The distribution of anemones on crabs that emerged from the experiments followed a very similar pattern as the one found prior to any manipulation. Both the right and left sides of the shell were preferred and contained the highest average number of *C. tricolor* which supports the hypothesis that *D. pedunculatus* places its symbiont in a determined pattern. The highest average number of *C. tricolor* at the end of all the experiments was consistently zone 4 of the shell, the left side, which was the closest to the large cheliped of *D. pedunculatus*. It could be possible that the area that requires the least work to get *C. tricolor* onto is the one closest to *D. pedunculatus* left cheliped, placement 4.

Even though the number of anemones present is correlated to survival of predation for some hermit crab species (Brooks 1988), *D. pedunculatus* did not place the maximum number of anemones presented under experimental conditions. A high number of anemones on the shell increases the rate of survival of the hermit crab (Brooks 1988). Since spacial distribution of *C. tricolor* also plays an important role in protection from predators (Brooks 1988), it is likely that *D. pedunculatus* places *C. tricolor* in a symmetrical way that protects most of the shell without necessarily needing a large number of them.

d) Conclusions

A distinctive set of behavioral patterns emerges from this study of *D. pedunculatus* to support that its association to *C. tricolor* is strongly established. Intraspecific competition in the form of one on one fights and stealing is shaped by a dominance of individuals based on size. *D. pedunculatus* actively seeks out its symbiont just like other hermit crabs symbiotic with sea anemones (Ross 1961, Ross 1970, Gusmao 2010). Since intraspecific competition is prevalent amongst *D. pedunculatus* even without the presence of a predator, *C. tricolor* could possibly be considered to be a valued resource in this population. The consistent stealing behavior implies that *C. tricolor* provides a benefit to *D. pedunculatus* like it has been shown to for other species

(Brooks 1993). These aggressive displays surrounding *C. tricolor*, in conjunction with a predictable pattern of their placement indicate that *D. pedunculatus* actively manipulates *C. tricolor* and could imply that it depends on the *C. tricolor* for survival. The behavioral patterns examined in this study contribute to understanding how delicate symbiosis are maintained in reef ecosystems. The delicate balance in these fragile ecosystems is affected by a combination of environmental pressures, and knowing more about mutualism brings light on how certain organisms evade certain pressures and thrive.

Future research

Although *D. pedunculatus* could rely solely on stealing and competition to obtain *C. tricolor*, hermit crabs are constantly changing shells (Abrams 1987) and the behavior of *D. pedunculatus* when changing shells is not very well established. It is possible that when there is shell changing, not all *C. tricolor* are transferred to the new shell and that stealing supplements the need for more symbionts. Another hypothesis could be that *D. pedunculatus* ages with the same *C. tricolor* obtained at a younger age, and that the *C. tricolor* grows on their shell while continuously being transferred to new shells. Studying the behavior of *D. pedunculatus* during a longer time frame in the wild could provide insight on the nature of its association with *C. tricolor* and how it affects the social structure of *D. pedunculatus* populations.

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LITERATURE CITED

- Abrams, P. 1987. An analysis of competitive interactions between 3 hermit crab species. *Oecologia* 72(2):233-247.
- Abrams, P. 1980. Resource partitioning and interspecific competition in a tropical hermit crab community. *Oecologia* 46(3):365-379.
- Abrams, P. 1987. Resource partitioning and competition for shells between intertidal hermit-crabs on the outer coast of Washington. *Oecologia* 72(2):248-258.
- Arnott, G., and R. W. Elwood. 2007. Fighting for shells: How private information about resource value changes hermit crab pre-behaviour. *Proceedings of the Royal Society of London Series B-Biological Sciences* 274(1628):3011-3017.
- Bach, C., B. Hazlett, and D. Rittschof. 1976. Effects of interspecific competition on fitness of the hermit crab *Clibanarius tricolor*. *Ecology* 57(3):579-586.
- Boucher, D., S. James, and K. Keeler. 1982. The ecology of mutualism. *Annual Review of Ecology and Systematics* 13:315-347.
- Brooks, W. 1988. The influence of the location and abundance of the sea-anemone *Calliactis tricolor* (Le Sueur) in protecting hermit crabs from octopus predators. *Journal of Experimental Marine Biology and Ecology* 116(1):15-21.
- Brooks, W. 1989. Hermit crabs alter sea-anemone placement patterns for shell balance and reduced predation. *Journal of Experimental Marine Biology and Ecology* 132(2):109-121.
- Brooks, W., L. Ceperly, and D. Rittschof. 1995. Disturbance and reattachment behavior of sea-anemones *Calliactis tricolor* (Le Sueur) - temporal, textural and chemical mediation. *Journal of Chemical Ecology* 21(1):1-12.
- Brooks, W., and C. Gwaltney. 1993. Protection of symbiotic cnidarians by their hermit-crab hosts - evidence for mutualism. *Symbiosis* 15(1-2):1-13.
- Cutress, C. and D. Ross. 1969. Sea anemone *Calliactis tricolor* and its association with the hermit crab *Dardanus venosus*. *Journal of Zoology* 158:225-&
- Gusmao, L. C. 2010. Systematics and evolution of sea anemones (Cnidaria):

- Actiniaria: Hormathiidae) symbiotic with hermit crabs. Ohio State University.
- Hay, M. E., J. D. Parker, D. Burkepile, C.C. Caudill, A. E. Wilson, Z. P. Hallinan. 2004. Mutualisms and aquatic community structure: the enemy of my enemy is my friend. *Annual Review of Ecology, Evolution, and Systematics* **35**:175-197.
- Hazlett, B. A. 1981. The behavioral ecology of hermit crabs. *Annual Review of Ecology and Systematics* **12**:1-22.
- Hazlett, B.A. 1978. Shell exchanges in hermit crabs - aggression, negotiation, or both. *Animal Behaviour* **26**:1278-1279.
- Imafuku, M., T. Yamamoto and M. Ohta. 2000. Predation on symbiotic sea anemones by their host hermit crab *dardanus pedunculatus*. *Marine and Freshwater Behaviour and Physiology* **33**(4):221-232.
- JMP, Version 7. SAS Institute Inc., Cary, NC, 1989-2007
- Karplus, I., G. C. Fiedler and P. Ramcharan. 1998. The intraspecific fighting behavior of the hawaiian boxer crab, *lybiaedmondsoni*: Fighting with dangerous weapons? *Symbiosis* **24**(3):287-301.
- Rittschof, D., S. McFarland, E. Stocker and W. Brooks. 1999. Movements of anemones symbiotic with hermit crabs: effects of light, gravity, flow and conspecifics. *Marine and Freshwater Behaviour and Physiology* **32**(4):193-205.
- Ross, D. M. 1960. The association between the hermit crab *eupagurus bernhardus* (L.) and the sea anemone *calliactis parasitica* (couch). *Proceedings of the Zoological Society of London* **134**(1):43-57.
- Ross, D. M. 1970. Commensal association of *calliactis-polypus* and hermit crab *dardanus-gemmatus* in hawaii. *Canadian Journal of Zoology* **48**(2):351-&.
- Ross, D. M. 1971. Protection of hermit crabs (*dardanus* spp) from octopus by commensal sea anemones (*calliactis* spp). *Nature* **230**(5293):401-&.
- Ross, D. M. 1979. Stealing of the symbiotic anemone, *calliactis-parasitica*, in intraspecific and interspecific encounters of 3 species of mediterranean pagurids. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* **57**(6):1181-1189.
- Ross, D. M. and L. Sutton. 1961. Association between hermit crab *dardanus arrosor* (herbst) and sea anemone *calliactis parasitica* (couch). *Proceedings of the Royal Society of London Series B-Biological Sciences* **155**(959):282-&.
- Ross, D. M. and L. Sutton. 1961. Response of sea anemone *calliactis parasitica* to shells

- of hermit crab *Pagurus bernhardus*.
Proceedings of the Royal Society of
London Series B-Biological Sciences
155(959):266-&.
- Ross, D. M. and L. Sutton. 1968. Detachment
of sea anemones by commensal hermit
crabs and by mechanical and electrical
stimuli. *Nature* **217**(5126):380-&.
- Schmitt, R. J. and S. J. Holbrook. 2003.
Mutualism can mediate competition and
promote coexistence. *Ecology Letters*
6(10):898-902.
- Vafeiadou, A., C. Antoniadou and C.
Chintiroglou. 2011. Symbiosis of sea
anemones and hermit crabs: Different
resource utilization patterns in the Aegean
sea. *Helgoland Marine Research* **1**:1-8
- Yasuda, C., Y. Suzuki and S. Wada. 2011.
Function of the major cheliped in male-
male competition in the hermit crab
Pagurus nigrofascia. *Marine Biology*
158(10):2327-2334.
- Yoshino, K., T. Koga and S. Oki. 2011.
Chelipeds are the real weapon: Cheliped
size is a more effective determinant than
body size in male-male competition for
mates in a hermit crab. *Behavioral Ecology
and Sociobiology* **65**(9):1825-1832.

APPENDIX A

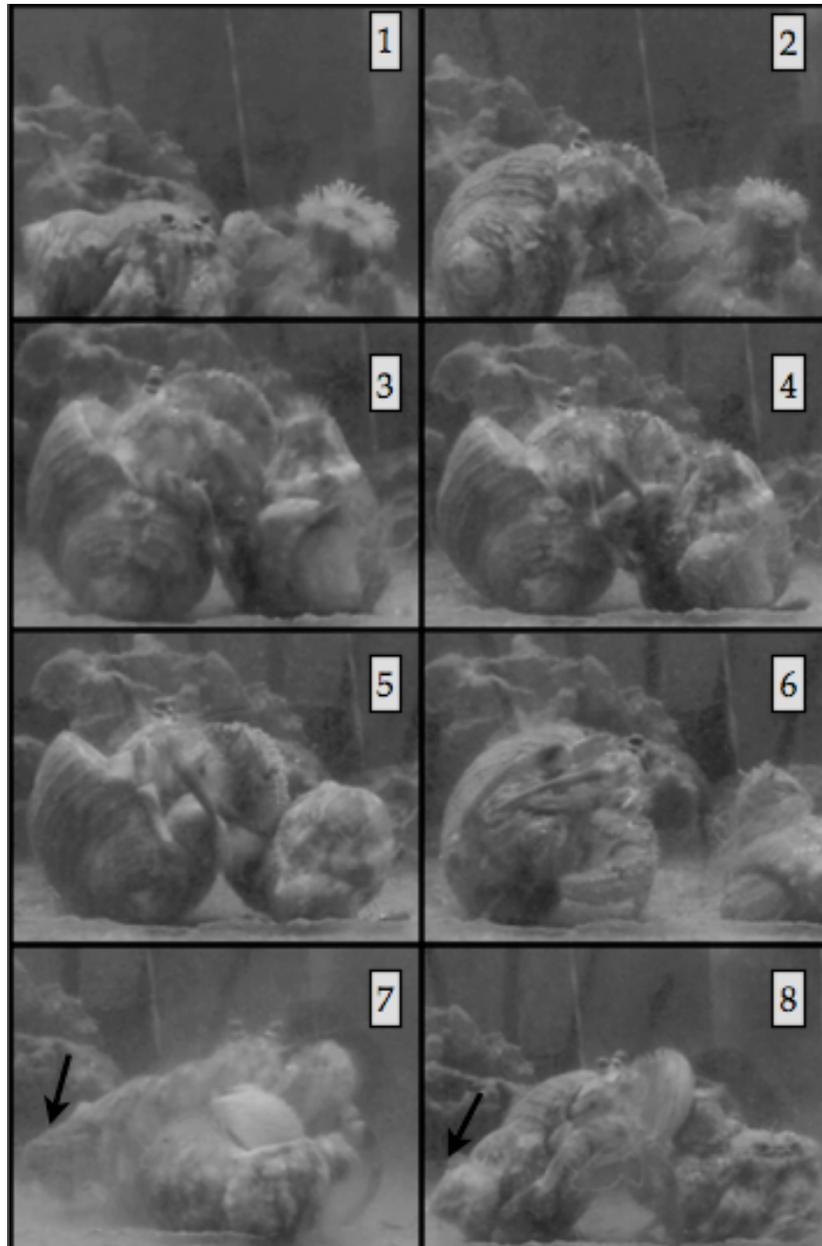


Fig A. Pictorial ethogram of the stealing behavior. Two *D. pedunculatus* individuals placed in in one tank (1), with the smaller one retreated into its shell. The larger *D. pedunculatus* mounts the smaller one (2), uses its chelipeds to relax *C. tricolor* and lessen its grip (3 & 4), rips it off (5) and finally attaches it to its shell (6). When the smaller *D. pedunculatus* comes out of its shell, the larger one uses its cheliped to dominate (7 & 8). The arrows point to *C. tricolor* attached to the larger *D. pedunculatus*.