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ONE IS THE LONLIEST NUMBER: THE EFFECTS OF ISOLATION ON THE BEHAVIORAL INTERACTIONS OF JUVENILE LAND HERMIT CRABS (COENOBITIDAE) FROM THE MOTUS OF MO'OREA, FRENCH POLYNESIA

*WITH AN APPENDIX SURVEYING THE HERMIT CRAB SPECIES PRESENT ON SELECT MO'OREAN MOTUS.

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Abstract. Hermit crabs interact with each other in a variety of ways involving spatial use (aggregations, migrations), housing (shells), mating, recognition of conspecifics, and food. To test if isolation from conspecifics affects the behavioral interactions of hermit crabs, crabs of the species *Coenobita rugosus* (Milne-Edwards 1837) of Mo'orea, French Polynesia were isolated from each other for two days, four days, six days, fifteen days, and twenty-two days. They were kept in individual opaque containers with separate running seawater systems to prevent them from seeing or smelling each other. Afterwards, the hermit crabs were put into a tank two at a time and their behavior was recorded and compared to the behaviors of non-isolated crabs. Behaviors looked at fell into two categories: 1) "social" interactions, meaning that the crabs reacted to each other's presence, and 2) "nonsocial" interactions, meaning that the crabs either ignored each other's presence or actively avoided behavioral interactions with other crabs. Results indicated that although "social" behavior showed a slight decreasing trend over time, it was not significant; however, the amount of "nonsocial" avoidance behavior seen increased significantly the longer crabs were isolated.

Key words: hermit crab, *Coenobita*, *Calcinus*, *Dardanus*, isolation, behavior, motu.

INTRODUCTION:

Hermit crabs, as crustaceans (Decapoda: Anomura), reveal many behaviors that provide insight into their interactions with conspecifics (Hazlett 1966, Hazlett 1981). Depending on the species involved and nature of the contact, they will exhibit a variety of behaviors including: aggregation (Tura 2000), stereotyped displays of chelipeds or pereopods to communicate intraspecifically during aggressive interactions (Hazlett 1966), chirping in certain *Coenobitids* (land hermit crabs) during battles over resources (Hazlett 1966), mate guarding and defending when

sex ratios are uneven (Wada S. 1999), and fights over the gastropod shells that they depend on to house their uncalcified vulnerable abdomens (Briffa M, Williams R. 2006). Interestingly, aggressive behaviors over food resources (detritus) are not normally observed, thereby leading to the tentative conclusion that food is not a driving force behind hermit crab social behavior (Hazlett 1981).

In order to interact with each other socially, hermit crabs need to be able to perceive each other and recognize conspecifics in their environments. They can detect each other through seawater via chemoreception (Diaz H, Forward Jr RB,

Orihuela B, Rittschof D. 1994; Gherardi, F., Tricarico, E., Atema, J. 2005) and crustaceans are known to have eyes capable of detecting shapes and a range of electromagnetic frequencies on land and in water (Johnson et al 2002, Barry et al 1974, Chiou T. et al. 2008). Hermit crabs are also capable of distinguishing familiar social partners by a binary recognition system that classifies crabs into familiar and unfamiliar categories (Gherardi F. and Tiedemann J. 2004a; Gherardi F. and Tiedemann J. 2004b); however, a hermit crab's ability to recognize individual crabs has not yet been studied (Gherardi, F. and Tricarico, E. 2007). Hermit crabs, in particular *Pagurus longicarpus*, are known to remember familiar social partners for 4 to 6 days (Gherardi F and Atema J. 2005). Furthermore, studies have shown that some related decapods, such as the crayfish *Cherax destructor*, are also able to recognize the faces of fight opponents, indicating the capability for certain crustaceans to have complex social interactions (Van der Velden, J. 2008). Considering the evidence that many hermit crabs interact with each other socially, studying the effects of the lack of social stimuli through isolation may provide many previously unrealized insights to their lives and ecology.

MATERIALS AND METHODS

Coenobita rugosus natural history

All work was conducted on juveniles of the land hermit crab *Coenobita rugosus* (H. Milne Edwards, 1837) (Coenobitidae) (identified from Poupin, J. Internet, and personal communication). *C. rugosus* is broadly distributed throughout the Indo-West Pacific including Japan (Bonin, Amami, and Okinawa), the Territory of Wallis and Futuna Islands, and French Polynesia. (Poupin, J., Internet). Within French Polynesia, *C. rugosus* is found in the

Austral archipelago (Raevavae); the Society Islands (Tahiti, Mo'orea); and the Tuamotu archipelago (Hikueru, Kaukura, Raraka, Raroia, Takume) (Poupin J. 1996). Hermit crabs in the family Coenobitidae are terrestrial and have developed many adaptations to help them live on land including having reduced gills, a planktonic larval stage, and a unique respiratory organ on their dorsal abdominal wall (the constraints of living in a shell limit the growth of branchiostegal lungs) (Greenaway 2003). Furthermore, many are known to drink seawater, fully submerge themselves in seawater, or sit in damp sand after rains (*C. rugosus*) in order to control their salt and water balance (Greenaway 2003). When threatened, Coenobitids are able to block the opening of their shell like an operculum due to adaptations of the left, dominant cheliped and the second ambulatory leg (Grubb 1971). This behavior is seen frequently displayed by *C. rugosus* during social interactions such as shell fights with conspecifics (personal observation). These adaptations within Anomura seem to be relatively recent in evolution with the earliest known Coenobitid fossils dating to the Lower Miocene (Greenaway 2003).

C. rugosus is also known to eat detritus, including decaying algae, fish, small invertebrates, dead giant tortoise (on Aldabra), and feces (Grubb 1971, Greenaway 2003). They are occasionally cannibalistic (Barnes 1997, personal observation).

Study site:

All *C. rugosus* were collected from the shoreline of Motu Tiahura (Figure 2) (17°29'14.33"S, 149°54'37.50"W, elevation 7 meters) on the north side of Mo'orea, French Polynesia (Figure 1) during the months of September through November 2008.



FIG. 1. Mo'orea, French Polynesia. Motu Fareone (A) and Motu Tiahura (B) can be seen in the northwest corner. Image taken from Google Earth.

Crab maintenance and preparation:

Isolation chambers consisted of individual opaque potting cups fitted with mesh and solid plastic bottoms with holes to provide water drainage. A piece of coral rubble was placed inside to increase the vertical distance a crab could crawl. Each isolation chamber had its own running seawater system and was sealed with a lid that had two holes drilled into it to allow the seawater to enter. All cups were elevated to prevent seawater pooling at the bottom. This was to avoid cross contamination of



FIG. 2. Motu Tiahura study site. All crabs were collected from an 80.5-meter length of beach on the east side of the motu. Image taken from Google Earth.

crab chemical cues. Every isolation chamber had fourteen to sixteen small holes drilled into the sides to allow proper air ventilation.

Crabs that were part of the communal crab experiments lived collectively in a large twelve-liter tank with constant running seawater and coral rubble on which to climb. The setup provided crabs the choice of full submersion in seawater or air. Many were observed to switch back and forth.

All crabs were fed a diet of cat food every third day and seemed to thrive on it, with many moving quickly to the location of food on feeding days. Housing was also cleaned every third day. Additionally, crabs were kept at ambient outside temperatures and humidities found in Cook's Bay on Mo'orea. *C. rugosus* have been found along the shores of Cook's Bay suggesting that the conditions are equally favorable between the two locations (personal observation).

Experimental design:

Isolation times consisted of two days, four days, six days, fifteen days, and twenty-two days. Ten replicates were conducted for every experiment. For each one of these intervals, two randomly selected isolated crabs were paired and placed in a two-liter tank at opposite ends. Crabs were only paired that came from the same isolation times, ie. only two six-day isolated crabs were paired together, never a six-day isolated crab and a two day isolated crab. To compare the results of the experiments, ten replicates were conducted in an identical manner with communally living crabs. Again, only communal crabs were paired with each other. The two-liter experimental tanks were filled with 0.24 liters (half a cup) of seawater, allowing the crabs to have access to seawater if needed without being fully submerged. The experiment tank was then thoroughly rinsed with seawater three times and refilled

between sequential experiments to remove all previous crab chemical cues.

Each crab pairing was observed for ten minutes at a time and behavior was recorded in a notebook. Videos of behavior were also taken at the end of each isolation period for three to five minutes. This was to record the initial behaviors of the hermit crabs upon reintroduction to a crowded (approximately 20 individuals) environment.

Statistical analysis:

Statistical analyses were followed according to the procedures described in Ambrose 2002. Linear regression and a Student's t test were used.

RESULTS

Behaviors observed

Hermit crabs of the species *C. rugosus* spent most of their time occupying the corners and edges of the experiment tank. They were rarely seen occupying space in the middle of the tank. Therefore, the times spent moving from one corner to another were not recorded as they were brief and seemed to have little relevance to the study.

Behaviors observed fell into two categories: 1) "social" interactions, meaning that the crabs reacted to each other's presence, and 2) "non-social" interactions, meaning that the crabs either ignored each other's presence or actively avoided behavioral interactions with other crabs. The first category of "social" interactions included climbing on each other, aggregation in the same corner, mutual feeling of each other with antennae while face-to-face, one crab following the other, ambulatory leg strikes against the other crab, rolling the other crab over, and grabbing the other crab's shell. The second category of "non-social" behavioral interactions included: full retraction into the

shell, fleeing from another crab, not moving while normally extended from the shell, and sitting in opposite corners of the tank (widthwise, lengthwise, and diagonally). These behaviors are described in more detail in Appendix B at the end of this paper.

Experimental results

The time crabs spent behaving socially and nonsocially differed significantly depending on how long they had been isolated (Figure 3).

The total amount of time crabs spent behaving socially with each other fluctuated throughout experiments with isolation times. There was a slight trend towards a decrease in social behavior as isolation time increased, but linear regression analysis on the data yields an R^2 value of almost zero ($R^2 = 0.02$) indicating very little significance, suggesting that there may be no pattern for the effects of isolation on hermit crab social

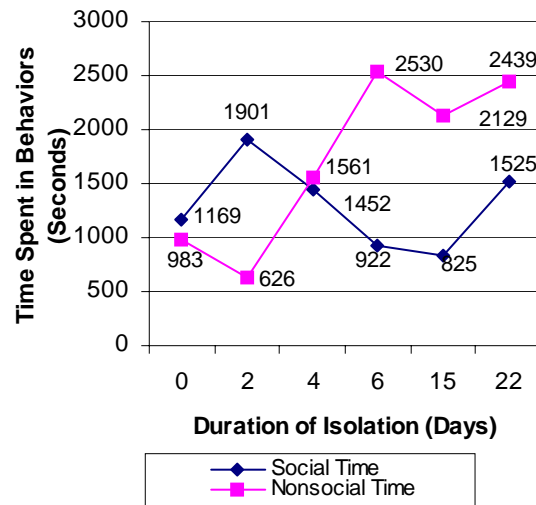


FIG. 3. Social versus nonsocial behaviors as a function of the time crabs spent isolated. The amount of time crabs spent displaying social behaviors fluctuates as the duration of isolation increases; whereas, the time spent in nonsocial behaviors increases rapidly as the duration of isolation increases.

TABLE 1. The results of a Student's t test for significance in data. Each p value corresponds to the total amount of time spent in social behaviors versus nonsocial behaviors as visualized in Figure 3. Communal living crabs and four days isolated crabs show no significant difference in social versus nonsocial behaviors.

	Communal living (0 Days)	2 Days Isolated	4 Days Isolated	6 Days Isolated	15 Days Isolated	22 Days Isolated
p Value	0.57	0.03	0.51	0.05	0.04	0.04

behavior (Figure 4).

However, as the duration of isolation periods lengthened, crabs behaved significantly more nonsocially, meaning that they avoided interactions with each other more than in experiments with less isolated crabs (Figure 3). The longer isolated crabs showed an increase in the duration of time they spent fully retracted in their shells, fleeing from another crab's approach, not moving, sitting in opposite corners of the tank whether in a widthwise, lengthwise, or diagonal position from the other crab. The trend in the data shows that nonsocial behavior spikes almost linearly from two days to six days of isolation and linear

regression analysis gives an R^2 value of one half ($R^2 = 0.53$) (Figure 4). This suggests that isolation does significantly affect hermit crab behavior by increasing avoidance behaviors amongst crabs. Furthermore, the results of a Student's t test for significance between the trends seen for social behaviors and nonsocial behaviors yielded p values of 0.05 and below, with the exception of communal living crabs and four day isolated crabs, suggesting that most social behavior data points are significantly different from nonsocial behavior data points (Table 1).

In addition to the increase in nonsocial behavior, personal observations noted that

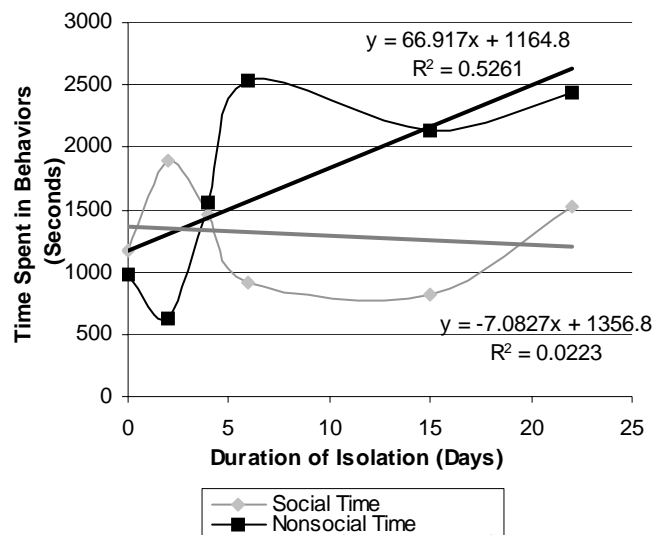


FIG. 4. Linear regression analysis of social versus nonsocial behaviors as a function of the time crabs spent isolated. Social behavior shows an R^2 value close to zero indicating that the changes in social behavior with increasing isolation are of little significance. The trend for nonsocial behaviors shows an R^2 value of close to one half indicating that the changes in nonsocial behavior with increasing isolation time are substantial.

the hermit crabs seemed to become more lethargic in their actions and each behavior previously seen in shorter isolation time experiments were lackluster in these. This was not quantified in these experiments since the intensity of interactions was not measured; however, these observations raised concerns that perhaps individual health was a confounding factor in these experiments.

As noted previously, crabs were fed every third day following protocol found in Gherardi 2005 and their isolation cups were cleaned thoroughly on this day to maximize the health of the crabs without sacrificing isolation time. Furthermore, they also had continuous access to fresh air and seawater. However, to investigate if the results of the experiments were possibly affected by ill health, a graph showing the total times spent in activity over periods of isolation was generated (Figure 5).

The total time crabs spent in active behaviors, despite an observed lethargy, increased as a function of time spent isolated. If poor health were a contributing factor to the increase in nonsocial behavior seen as isolation times increased, then one

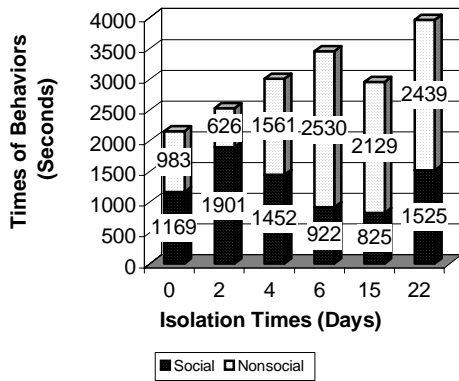


FIG. 5. Total activity of crabs as a function of isolation time. White bars represent time spent in nonsocial activity; black bars represent time spent in social activity. Crabs show a general trend of increasing total activity the longer they have been isolated.

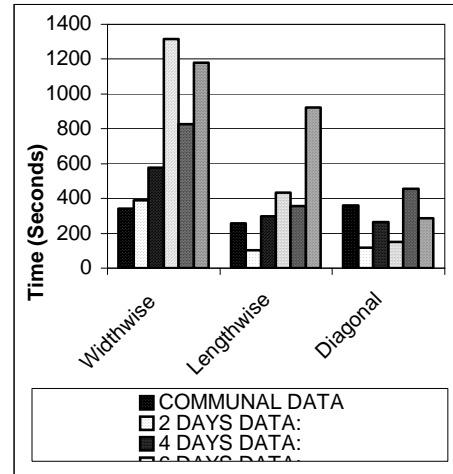


FIG. 6. Total time spent in corners per experiment. Crabs seem to prefer the widthwise position in the tank. The lengthwise and diagonal positions, depending on the experiment, are favored interchangeably for the next most preferred.

might expect that the total time hermit crabs spent actively demonstrating behaviors would decrease.

An unexpected result was the demonstrated preference for occupying specific regions of the experiment tank. As part of “nonsocial” behavior, the amount of time hermit crabs spent in separate corners of the tank was recorded. This included the corners that were widthwise apart in the tank, lengthwise apart in the tank, and diagonally apart in the tank (see appendix B for diagrams of these distances). Throughout most experiments, hermit crabs showed a preference for occupying the corners of the tank that were widthwise apart (Figure 6).

These results on hermit crab preferences for occupying a particular position in the tank were unanticipated and are hard to explain. Perhaps hermit crabs prefer to be a certain distance apart from each other after periods of isolation. Further research should be conducted to see if this observation yields more results. It would be

particularly interesting if the same preferences, perhaps measured in distances apart rather than corners, were observed in a more natural environment than an experiment tank.

Conclusions

The trend seen for the effects of isolation on hermit crab behavior yielded three interesting results. First, hermit crabs do not interact with each other any less socially when confined in the same space with each other after a period of isolation than before. Second, hermit crabs do actively avoid each other more after a period of isolation as seen from the increase in time spent demonstrating nonsocial behaviors. Third, as part of hermit crab nonsocial behavior, crabs favored occupying corners of the tank widthwise apart from each other, possibly due to a preference for being a certain distance apart, in this case approximately fifteen centimeters.

DISCUSSION:

The results that nonsocial behavior increases and social behavior does not show any significant trend over isolation periods are interesting in that one might think that they would have to inversely decrease. However, as seen from the results, this is not necessarily the case when the times of individual behaviors are recorded over a ten-minute interval. Each behavior was mutually exclusive; however, the combination of time spent in social behaviors and time spent in nonsocial behaviors did not necessarily sum up to the full ten minutes of observations since times spent moving from one corner to another were not recorded unless some other significant behavioral interaction took place simultaneously.

When confined in a small space, hermit crabs after a period of isolation show that they do not necessarily interact with each

other any less socially. However, since the amount of nonsocial avoidance behaviors did increase, more research should be done to see if hermit crabs, perhaps in the wild, would show a decrease in social behavior when occupying a less confined space.

Another interesting outcome of these experiments is that the results contradict the findings in Pessani 1992 with the hermit crab species *Clibanarius erythropus*. Pessani found that after fifteen days of isolation, *C. erythropus* social behavior increased upon reintroduction to one another. The discrepancy in the results could be due to several factors, the most likely of which could be that these two species react differently to periods of isolation. Locality, specific behaviors examined, and the time of year could also be factors in the disagreement of the two outcomes. An excellent future study could focus expressly on using the same behaviors to measure how these two species interact with each other intraspecifically and interspecifically after the effects of isolation.

Additionally, the results of the four-day isolation experiments indicate another interesting parallel with the literature on hermit crabs. At four days of isolation, social behaviors and nonsocial behaviors are demonstrated equally by the crabs involved (Figure 3), and a p value of 0.51 confirms this (Table 1). In a similar study, Gherardi and Atema 2005, the length of a hermit crab's (*Pagurus longicarpus*) memory of a social partner was tested. They analyzed the times crabs spent in social interactions with each other and how much they varied over a period of separation time from the same social partners. Their results indicated that the limit of a hermit crab's memory of social partners is about four days. They found that after this time, the crabs interacted with a previous social partner in no discernibly different way than with a crab they had never met before. These results and the results of the four-day isolation experiments in this paper suggest

that hermit crabs may interact with new social partners equally as much as they will avoid them. This raises many interesting questions regarding how hermit crabs interact with new social partners and how this affects hermit crab ecological communities as a whole when new crabs are introduced and familiar ones removed. If many crabs are removed from beaches, like they are for the pet trade, hermit crabs may interact with each other differently, which may, in turn, affect how their communities interact with their environments. If there are indeed ramifications, this could seriously affect the ecology of the coastal marine ecosystems in which they live since hermit crabs play a vital role in cleaning up their environments by acting as detritivores and shell “recyclers”. Further research needs to be done to investigate how hermit crab communities that have been impacted by the pet trade, or by other artificial means that impose isolation on certain members of their community, interact with their environment.

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APPENDIX A

A PRELIMINARY SURVEY OF THE HERMIT CRAB SPECIES PRESENT ON SELECT MO'OREAN MOTUS

LOCATIONS

All crabs were collected from Motu Ahi, Motu Fareone, and Motu Tiahura (Figure A1). All motus were searched as thoroughly as possible via walking, turning over rocks and coral heads, snorkeling, and free diving in the attempt to find every hermit crab species present on the motus. All work was conducted within the main barrier reef. Private property, when permission could not be attained, was excluded from the survey locations.



FIG. A1. Mo'orea, French Polynesia with motu survey sites labeled A: Motu Fareone, B: Motu Tiahura, and C: Motu Ahi.

All crabs were collected between September and November 2008 and the following compilation lists all the species found organized by motu. Where species duplicate, the species name is listed with locale information and a reference to the original motu on which it was found. It is auspicious that most hermit crabs in the South Pacific have distinct color patterns and markings that are diagnostic to species level (personal communication with Poupin, J.). Therefore, color information is listed along with any important markings to help discriminate between species as well as a black and white photograph of each. All photos are the property of Albert Park.

Calcinus elegans (H. Milne Edwards, 1836) (Diogenidae)

Calcinus elegans is marine and is found along the ocean side of the motu within the lagoon in shallow water. The water here tends to be colder than the inner lagoon sides of the island and the waves more frequent with bigger surges (personal observation). *C. elegans* of the Indo-Pacific has vivid blue bandings alternating with black on the ambulatory legs and vivid blue eyestalks; while, individuals from Hawaii have different (orange) colorations (Poupin, J. Internet). The eyes themselves of the Indo-Pacific crabs are blue. The antennae and antennules are orange. The shield ranges from a pale green-blue to cream. This individual was found in the ocean-side lagoon within one meter of the coral rock platform on the east side of the motu (Figure A2).



FIG. A2. *Calcinus elegans*.

Calcinus laevimanus (Randall, 1840) (Diogenidae)

Calcinus laevimanus is marine and found mostly in the very shallow lagoon waters within one to two meters of the beach. They were most often found in aggregations under small rocks, small living coral heads, or fossilized coral chunks. The majority of the body visible from the shell is brown. They have two white horizontal stripes at the distal most ends of their ambulatory legs and their dominant cheliped is brown with white encircling the pinching portion of the cheliped. Their eyestalks alternate colors from the base to the distal ends: orange, blue, to orange in thick horizontal stripes. The eyes themselves are blue. The antennae are orange and the antennules are orange and blue in alternating horizontal stripes. This individual was found hidden in rubble in very shallow water along the east ocean side of the island in the lagoon (Figure A3).



FIG. A3. *Calcinus laevimanus*.

Calcinus latens (Randall, 1840) (Diogenidae)

Calcinus latens is marine and was found from the sheltered shallow, warm, and calm lagoon waters to the colder more exposed ocean side of the motu. They are green to gray in color and they have purple eyestalks. The eyes are black and oftentimes have small white dots. The antennae are yellow and



FIG. A4. *Calcinus latens*.

the antennules are blue terminating with orange tips. The chelipeds and pereopods have a gradual change in color from the base to the distal ends: they start out green, move to a light purple, and switch to a light green by the third segment. Then there is a dark purple band that encompasses the fourth segment and the legs terminate at the fifth segment with a white band. They were found by living coral heads as well as under rocks. This individual was found walking exposed on the top of a coral head with no rocks or other shells to camouflage it on the east ocean side of the motu within one meter of the fossil coral rock platform (Figure A4).

Coenobita perlatus (H. Milne Edwards, 1837) (Coenobitidae)

Coenobita perlatus is terrestrial and was found amongst the coral rubble lining the beaches circumventing the motu. Larger adults were also found on the trees and shrubs (*Cocos*, *Pemphis*) farther inland and are much redder than the juveniles. The juveniles (pictured here) are pale pink to cream colored with pink to red horizontal stripes just distal to the joints of the ambulatory legs (pereopods). The eyestalks, typical of all Coenobitids, are triangular in shape in that they are thin at the base and flare out at the terminal ends. The eyes are brownish red and are shaped like half-moons. The antennae and antennules are pink. This individual was found on the south beach in the coral rubble (Figure A5).



FIG. A5. *Coenobita perlatus*.

Coenobita rugosus (H. Milne Edwards, 1837) (Coenobitidae)

Coenobita rugosus is terrestrial and was found among the coral rubble and debris lining the beaches circumventing the motu. They occur sympatrically with *C. perlatus* (personal observation). Adults tend to move inland and inhabit drier areas than adults of *C. perlatus* (personal communication with Poupin, J.). Adults are a deep brown color and were also found to climb trees. Juveniles (pictured here) are cream in color with many blotches of brown covering their bodies. They have brown vertical stripes on the ambulatory legs (pereopods) spanning the length of each leg segment between joints. Their eyes and eyestalks are brown and, like *C. perlatus*, the eyes are triangular in shape in that they are thin at the base and flare out at the terminal ends. The antennae and antennules are brown. Oftentimes there is a brown spot on the lateral side of the dominant left cheliped. This individual was found on the south beach in the coral rubble (Figure A6).



FIG. A6. *Coenobita rugosus*.

Dardanus lagopodes (Forskål, 1775) (Diogenidae)

Dardanus lagopodes is marine and are most often found in medium depth (one to three meters) lagoon water by the motus. (Two were found at 26 meters while scuba diving near the motus [the crater dive site]; however, this was outside the barrier reef.) They are purple in color and are covered in white and purple setae. The eyestalks are white and have a band of bright yellow at the terminal end adjacent to the eyes. The eyes are black and half-moon shaped. The antennae and antennules are yellow and flanked with two lengthwise black stripes. There are two purple blotches in between the second and third segments of the pereopods. This individual was found on the east ocean side of the motu within 2 meters of the fossil coral rock platform (Figure A7).



FIG. A7. *Dardanus lagopodes*

Motu Fareone

Note: Since Fareone and Tiahura are at a maximum distance of .28 kilometers and a minimum of .09 kilometers apart, it is likely most crabs found at one site may also occur at the other.

Calcinus laevimanus (Randall, 1840) (Diogenidae)

Found in the east lagoon under a small rock in an artificial rock jetty (approximately 4 meters long). This individual was aggregated with many conspecifics and individuals of *C. laevimanus*, *C. seurati*, and *Clibanarius humilis*. (Figure A3 in Motu Ahi.)

Calcinus latens (Randall, 1840) (Diogenidae)

Found in the east lagoon under a small rock in an artificial rock jetty (approximately 4 meters long). This individual was aggregated with many conspecifics and individuals of *C. laevimanus*, *C. seurati*, and *Clibanarius humilis*. (Figure A4 in Motu Ahi.)

Calcinus seurati (Forest, 1951) (Diogenidae)

Calcinus seurati is marine and found mostly in very shallow lagoon waters within one to three meters of the beach. They are similar in appearance to *C. laevimanus*, except that these have entirely brown to cream colored chelipeds (no white blotch at the terminal end). They also tend to be a much lighter brown than *C. laevimanus*. They have orange antennae and orange antennules with blue at the bases. Their eyestalks also alternate colors in horizontal stripes starting from the base: orange, blue, to orange at the terminal ends. The eyes are blue. This individual (missing a 3rd pereopod) was found in the east lagoon under a small rock in an



FIG. A8. *Calcinus seurati*.

artificial rock jetty (approximately 4 meters long). This individual was aggregated with many conspecifics and individuals of *C. latens*, *C. laevimanus*, and *Clibanarius humilis* (Figure A8).

Clibanarius humilis (Dana 1851) (Pylochelidae)

This is the only species found in the motu in this survey from the family Pylochelidae. All crabs in this family have equally sized chelipeds, ie. one claw is not larger than the other (personal communication with Poupin, J.). They are brown in color and have orange flanking the proximal ends of the segments at the pereopod joints. They have orange antennae and green antennules with orange at the tips. Their mouthparts are noticeably lime green. They have thin white stripes encircling the proximal ends of the chelipeds and white spots scattered over the distal ends. They were found in the east lagoon under a small rock in an artificial rock jetty (approximately 4 meters long). This individual was aggregated with many conspecifics and individuals of *C. laevimanus*, *C. latens*, and *C. seurati* (Figure A9).



FIG. A9. *Clibanarius humilis*.

Coenobita perlatus (H. Milne Edwards, 1837) (Coenobitidae)

Found on circumventing the island in the coral rubble of the shores. (Figure A5 in Motu Ahi.)

Coenobita rugosus (H. Milne Edwards, 1837) (Coenobitidae)

Found on circumventing the island in the coral rubble of the shores. (Figure A6 in Motu Ahi.)

Dardanus lagopodes (Forskål, 1775) (Diogenidae)

Found in 2.5 meters of water in the pass between Motu Fareone and Motu Tiahura. This individual was found walking in the sand in between two large coral heads within 6 meters of the northeast side of Motu Fareone. (Figure A7 in Motu Ahi.)

Motu Tiahura

Calcinus elegans (H. Milne Edwards, 1836) (Diogenidae)

Found in the ocean-side north lagoon near corals and adhered to the vertical edge of the fossil coral rock platform at the waterline. (Figure A2 in Motu Ahi.)

Calcinus laevimanus (Randall, 1840) (Diogenidae)

Found under small rocks and coral heads in the sheltered shallow lagoon waters within one meter of shore in all lagoons except on the north ocean side of the motu. (Figure A3 in Motu Ahi.)

Calcinus latens (Randall, 1840) (Diogenidae)

Found under small rocks and coral heads in the sheltered shallow lagoon waters within one meter of shore in all lagoons. (Figure A4 in Motu Ahi.)

Calcinus seurati (Forest, 1951) (Diogenidae)

Found as the only hermit crab species present in semi-evaporated tide pools on the fossil coral platforms on the north ocean side of the motu. The water here was very shallow (approximately 0.15 m deep), hot, and had a high salt content, presumably due evaporation (personal observation). (Figure A8 in Motu Fareone.)

Coenobita perlatus (H. Milne Edwards, 1837) (Coenobitidae)

Found amongst the coral rubble lining the beaches circumventing the motu. Larger adults were also found on the trees and subs (*Cocos*, *Pemphis*) farther inland. (Figure A5 in Motu Ahi.)

Coenobita rugosus (H. Milne Edwards, 1837) (Coenobitidae)

Found amongst the coral rubble lining the beaches circumventing the motu. (Figure A6 in Motu Ahi.)

Clibanarius humilis (Dana 1851) (Pylochelidae)

Found under small rocks and coral heads in the sheltered shallow lagoon waters within one meter of shore in all lagoons. (Figure A9 in Motu Fareone.)

Dardanus lagopodes (Forskål, 1775) (Diogenidae)

Found in all lagoon waters one meter deep until the barrier reef. (Figure A7 in Motu Ahi.)

Dardanus megistos (Herbst, 1804) (Diogenidae)

Dardanus megistos is marine and was found in medium depth (one to three meters) water in the lagoons surrounding the motu. It is orange and red with red eyestalks that terminate in a small band of black and a small band of white adjacent to the eye. They eye is black and half-moon shaped. There are red setae and white circular dots lined with black covering the body including the uncalcified abdomen. The antennae are red at the base and switch to white at the joint. The antennules are a deep orange at the base and gradually fade into yellow. This individual was found in a car tire in approximately one meter of water off the east lagoon side shore of the motu (Figure A10). It was found with *C. latens*, *D. lagopodes*, *D. scutellatus*, and an unknown shrimp living in a circular burrow.

Dardanus scutellatus (H. Milne Edwards, 1848) (Diogenidae)

Dardanus scutellatus is marine and was found in medium depth (one to three meters) water in the lagoons surrounding the motu. It is mottled and has varying colors from cream to purple to brown. The eyestalks are white and terminate with a yellow



FIG. A11. *Dardanus scutellatus*.

band adjacent to the eye. They eyes are black and silver. The antennae are black at the base and have two lengthwise stripes of white until proximal to the joint. Distal of the joint, the antennae are clear to yellow in color. There is also yellow flanking the joint on the antennae. The antennules have the same pattern except that they terminate in all yellow ends. They are lightly covered in purple setae; however, this is much less so than in *D. lagopodes* and *D. megistos*. This individual was found in a car tire in approximately one meter of water off the east lagoon side shore of the motu (Figure A11). It was found with *C. latens*, *D. lagopodes*, *D. megistos*, and an unknown shrimp living in a circular burrow.

APPENDIX B

A DESCRIPTION OF BEHAVIORS SEEN BY COENOBITA RUGOSUS DURING ISOLATION EXPERIMENTS

"Social" Behaviors:

1. Climbing on each other:

One crab climbing on the other crab. This behavior was timed and recorded whether or not the crabs were in the same corner, ie. some measurements were taken when crabs were halfway between corners. If crabs were in the same corner and climbing on each other, the behavior was recorded as climbing on each other.

2. Face-to-face interactions:

Crabs facing each other head on. Oftentimes, the crabs touch their antennae and antennules to the other's body. This behavior varied as to whether mutual antennae touching or just one individual touching the other with antennae occurred. Again, if this occurred while crabs were located in the same corner, the behavior was recorded as a face-to-face interaction for its duration. Afterwards, if a face-to-face interaction ended and the crabs remained in the same corner, the subsequent time was recorded as a same corner aggregation.

3. Same corner aggregation:

Both crabs occupied the same corner without climbing on each other. Crabs had to be within one and a half body lengths of each other to still be considered part of the same corner. This behavior is called an aggregation despite the fact that only two crabs were involved due to some preliminary studies conducted with 3 crabs, 4 crabs, and 20 or more crabs. These studies showed very similar behaviors overall to the 2 crabs experiments conducted here, including mass aggregations of crabs in the same corner for varied amounts of time.

4. One crab following another:

One crab following another's movements usually at a distance of a few body lengths. This often involved the pursuer crab stopping when the pursued crab stopped. After a stop, it was observed that sometimes the pursuing crab would abandon its course when the other crab moved again; whereas, other times, the pursuing crab would continue to follow the pursued crab. No data was taken as to how often one approach was utilized over the other. This would be an interesting point for further research.

5. Ambulatory leg strikes:

One crab using a walking leg (2nd and 3rd pairs of legs) to strike at the other crab. This was the only behavior noted that was recorded in instances instead of time.

6. Rolling:

One crab holding onto the other's shell and rolling that crab over. This is different from "shell rapping" (Gherardi F, Atema J. 2005) in that the aggressor crab does not rap its own shell against the shell of the defending crab.

7. Grabbing:

One crab using its chelipeds to hold onto the shell of the other crab. Reaching into the other crab's shell was never observed.

"Nonsocial" Behaviors:

1. Shell hiding:

One crab fully retracted into its shell showing no interactions with the other crab.

2. Fleeing:

One crab scuttling away quickly from the approach of the other crab. This behavior lasted for varied amounts of time, usually between three to five seconds.

3. Not moving:

One crab not moving around while not retracted into its shell. Appendages may be moving.

4. Opposite corners (widthwise):

Both crabs occupying two different corners in the tank widthwise apart from each other (approximately 15 cm). Looking at a rectangular tank from above, this would include both the close and far widthwise corners (Figure B1).

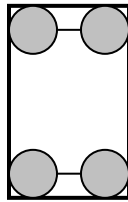


FIG. B1. The view of a tank from above. The gray circles represent areas that the hermit crabs may occupy. Lines represent the distance (approximately 15 cm) between two crabs. Figure not to scale.

5. Opposite corners (lengthwise):

Both crabs occupying two different corners in the tank lengthwise apart from each other (approximately 25 cm apart). Looking at a rectangular tank from above, this would include both the left and right lengthwise corners (Figure B2).

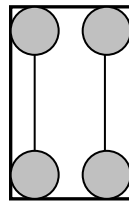


FIG. B2. The view of a tank from above. The gray circles represent areas that the hermit crabs may occupy. Lines represent the distance (approximately 25 cm) between two crabs. Figure not to scale.

6. Opposite corners (diagonally):

Both crabs occupying two different corners in the tank diagonally apart from each other (approximately 29 cm apart). Looking at a rectangular tank from above, this would include both possible diagonal corners (Figure B3).

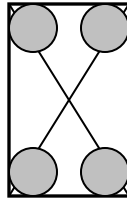


FIG. B3. The view of a tank from above. The gray circles represent areas that the hermit crabs may occupy. Lines represent the distance (approximately 29 cm) between two crabs. Figure not to scale.