STUDIES ON THE FAUNA OF CURAÇAO AND OTHER CARIBBEAN ISLANDS: No. 88.

SOCIAL BEHAVIOR OF THE PAGURIDAE AND DIOGENIDAE OF CURAÇAO

by

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INTRODUCTION

The number of unanswered questions and untouched problems in the study of animal behavior is very large. This is particularily true in the sub-discipline of animal communications. The fact that the behavior of one animal can change the behavior of a second animal is too often only tacitly implied or stated without amplification. Before the "language" of any organism can be studied as a behavioral phenomenon or the communications systems of a phylogenetic series studied as an evolutionary phenomenon, it is essential that the basic behavioral biology of the species or group be examined and described. The present work is an attempt to fulfill this latter requirement.

The social behavior of the marine hermit crabs (Paguridae and Diogenidae) of Curaçao, N.A., is described and in part analyzed. In addition to providing this basis, data have been gathered, which upon analysis have elucidated certain features of the aggressive communications systems of eight species of hermit crabs.

From the data gathered, the following aspects of hermit crab behavior are described: the behavior patterns of these crustaceans, as observed under laboratory and field conditions, the results of a number of experimental analyses of behavioral stimuli, and the results of some preliminary investigations of dominance hierarchies.

The social behavior of hermit crabs has taken very little space in zoological literature. However, much has been written about the behavior and physiology of individual crabs from the viewpoint of shell habitation (see REESE 1962a, 1963), neurophysiology (ALEXANDROWICZ 1952, STIEVE 1963), sensory physiology (BOHN 1902, GOLDSMITH 1918, BROCK 1927, KOLLER 1927, TEN CATE 1930, and others), symbiotic relationships (BROCK 1927, BRIGHTWELL 1951, 1953, BERNER 1953) and feeding behavior (ORTON 1927, BROCK 1930). JACKSON (1913) produced a rather good study of general anatomy and biology as did MAKAROV (1938) in his introduction to a systematic treatment of the Russian Paguridae.

BOUVIER (1892) and BOHN (1903) briefly mentioned that hermit crabs do fight among themselves for shells. ALLEE & DOUGLIS (1945) observed that specimens of *Pagurus longicarpus* fight one another for shells and that there was a dominance order in this fighting, insofar as larger crabs always extracted smaller crabs. Their observations were confined mostly to interactions in which one individual was without a shell. They observed that the aggressive (shell-less) crab "grasps the chelae and the legs of the occupant with one of its large pinchers jerks quickly, and so removes the smaller crab, and often throws it some distance away." REESE (1962b) carried out more extensive observations of shell fights between individuals of *Calcinus laevimanus*, but again, one of the interacting crabs was artificially shell-less.

Reports of sexual behavior also have been few. MATTHEWS (1959) suggested that copulation in *Pagurus prideauxi* is not necessarily confined to the short period following female ecdysis. He found spermatophores on immature females, the outer cuticular membrane of living, embryonated ova attached to the pleopods and on immature males. MATTHEWS attributed this diversity of recepients of spermatophores to "indiscrimination of the part of the male [which] proposes he may copulate with any hermit crab of his species that he can physically overpower." MACGINITIE & MACGINITIE (1949) and MATTHEWS (1956) mention that male hermit crabs are sometimes seen dragging females about prior to copulation.

BOTT (1940) reported that in *Pagurus prideauxi*, a male remains with the female during the period of moulting and until egg laying. BRANDES (1897) mentioned that the male *P. prideauxi* holds the tarsal segment of the second right ambulatory leg of the female with his left cheliped prior to copulation. BRANDES observed that during copulation, the major cheliped is held over the female (in a protective fashion) as they both ease partially out of their shells. COFFIN (1960) noted that the male *Pagurus samuelis* held the shell of the female with his minor cheliped for a number of hours prior to the one-second long copulation. The male waved the shell of the female back and forth, bumping it against his shell or body and/or twisting his body and shell while pressing against the shell of the female. During copulation, both eased out until only 2/3 of their abdomens remained in their shells. KAMALVENI (1949) reported on the copulation of *Clibanarius olivaceous*. However, the observed pairs were without shells artificially and their 90 minute pairing, with ambulatories intertwining may have been aberrant. He also stated that recently moulted females generally attracted the attention of males, but gave no details.

Although the literature pertaining directly to the social behavior of hermit crabs is limited, many of the phenomena mentioned in this paper have been observed in other crustaceans. DOUGLIS (1946) reported straight-line dominance orders in the lobster, *Homarus americanus*. BOVBJERG (1953, 1956) and LOWE (1956) have investigated the development of aggression and straight-line dominance orders in several species of crayfish. Both size and sex, predominantly the former, were found to be factors in determining the order in a hierarchy.

Although many authors have mentioned that members of a given crustacean species may fight with conspecific individuals, the manner of fighting is usually not described nor the signal-display level of aggression recognized. One notable exception has been the work of CRANE (1941a, 1943, 1957, 1958) and others on the conspicuous movements of the major cheliped of male fiddler crabs, *Uca* species. CRANE has observed that these courtship movements signal territory holding to other males and thus tend to keep them from intruding. In additon, CRANE (1958) has described a number of displays in *Uca maracoani* which she believes act as communicatory signals to conspecific individuals concerning the psycho-physiological state of the displaying crab. Another group in which a signal-display level of aggressive communication has been recognized is the snapping shrimp, *Alpheus* and *Synalpheus* (HAZLETT & WINN 1962).

Both the sight of the open snapping claw and the jet of water produced by a "snap", act as retreat-causing stimuli, thereby avoiding actual physical contact between interacting individuals. Physical combats without damage are frequent among individuals of the common shore crab, *Pachygrapsus crassipes* (HIATT 1948, BOVBJERG 1960) and the grapsoid crab, *Dotilla mictyroides* (TWEEDIE 1950). ALCOCK (1892) and CRANE (1941b) reported that burrow-occupying *Ocypode* crabs produce a twittering sound when an intruding conspecific individual enters its burrow. Presumably, substrate detection of this sound tends to induce retreat in the intruder.

The presence of chemical attraction and/or excitation of males by ripe females has been supposed for a number of lower crustaceans – *Pandalus danae* (NEEDLER 1931), *P. borealis* (CARLISLE 1959), *Palaemonetes vulgaris* (BURKENROAD 1947), *Leander serratus* (FORSTER 1951), *Crangon crangon* (NOUVEL 1939), *Orchestia gammarella* (WILLIAMSON 1954) - but proven for none. A wide-spread characteristic among crustaceans is the restriction of time when mating takes place. In the great majority of species investigated, copulation is restricted to a short period following a female moult – *Cancer pagurus* and *Carcinus maenas* (WILLIAMSON 1902) and *Neptunus pelagicus* (CHHAPGAN 1956). Often the male crab carries the female about for hours or days prior to her moulting, probably to assure that he is present when she is ready to mate – *Carcinus maenas* (BROEKHUYSEN 1937), *Callinectes hastatus* (CHIDESTER 1911) and *Gammarus pungens* (HOMES 1903).

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Portions of this work were presented to the Department of Biology, Harvard University, in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

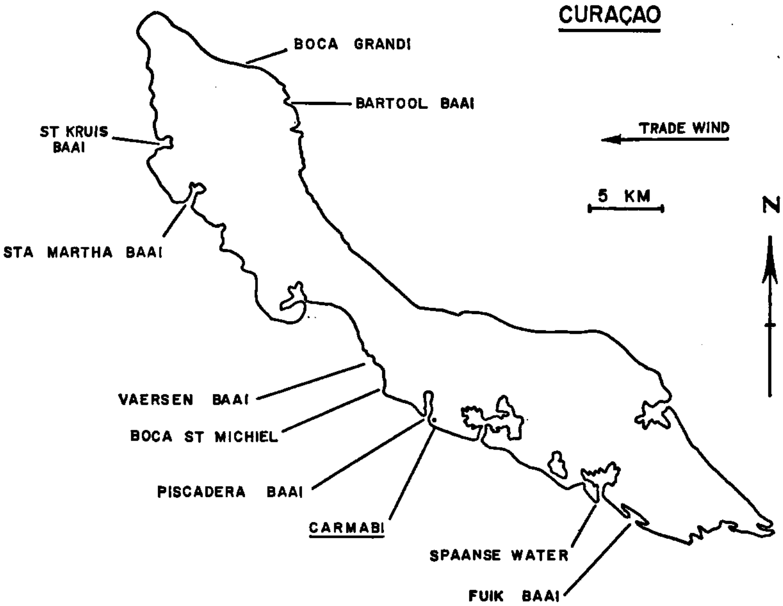


Fig. 1. Location of collecting-study areas around CURAÇAO, N.A.

COLLECTING AREAS ON CURAÇAO

Curaçao, N.A., is a medium-small island with an area of about 430 square kilometers, about 65 km off the coast of Venezuela (Fig. 1). A constant wind from the east maintains strong wave action on the north-east side of the island. Even those sheltered bays and inlets present here are, for the most part, characterized by heavy wave action. In addition, the inshore bottom is made up of relatively smooth, large, flat rocks, e.g. Boca Grandi and Bartool Baai.

The majority of the collecting-study areas were on the south coast of Curaçao. The greatest amount of work was done in the shallow waters directly in front of the Caribbean Marine Biological Institute (Carmabi), adjacent to Piscadera Baai, which may be called Piscadera Buiten Baai (Piscadera Outer Bay). Wave action there is moderate, and the gently sloped bottom is composed of detritus-covered rocks and coral rubble. This rocky condition extends out for 15–20 meters from shore. There is then an area of sandy bottom which gives way to coral formations at the edge of a sharp drop-off. The drop-off starts at a depth of about eight meters and descends rapidly.

The entrance to the Piscadera Binnen Baai (Piscadera Inner Bay) is a relatively shallow channel, less than three meters deep at one point. It has steeply sloping sides made up of small to medium, rather clean rocks which offer refuge to many organisms. As the tide goes out and until it rises again, the channel and the area in front of and to the west of the entrance of the bay are greatly discolored by the emptying of the Inner Bay. This tidal movement surrounds the organisms in the entrance in a relatively thick suspension of organic matter.

Piscadera Binnen Baai is a large body of water, covering an area of about 0.6 square kilometer, with an average depth of about 3 meters. Due to the concentration of civilization around it and the topography of its narrow entrance, the bay has a rich suspension of organic particles in its waters. The majority of the shores of the inner bay is composed of mangrove mudflats which are partially exposed at low tide.

The entrance to Spaanse Water is much wider and deeper than that of Piscadera Baai. It is about 35 meters wide and over 10 meters deep. The eastern shore is very steep and made up of medium to small rocks and pebbles. The western shore is relatively gently inclined from about eight meters upward. Proceeding inward, the bottom of the west slope changes from a very large dense growth of elkhorn coral (*Acropora palmata*), to a shallow flat of eelgrass, to a clear sandy bottom. Spaanse Water itself, *viz.* its inner bay is a 3½ × 1½ kilometer large body of relatively clear water. Its inlets, such as Brakkeput, are shallow mangrove mudflats but the water is clearer than of Piscadera Baai mudflats.

The entrance to St. Martha Baai is also steeply banked and made up of small pebbles and rocks. The area just outside the bay is a shallow shelf with heavy coral growth and relatively rough surf action.

Vaersen Baai is a moderately sloped, open inlet. The bottom is covered with medium size detritus-covered rocks. Surf action is moderate.

Boca St. Michiel (St. Michiel's Baai) is an open area with medium-light surf action. The first 5–6 meters of the bottom extending out from from the waterline is a broad, gently sloped rock shelf, covered with detritus and algal growth. A number of artificial piles of large rocks project seaward on this shelf. At about one and a half meters water depth, the shelf drops about 50 cm to a sandy bottom, which extends out to rather deep water.

RELATIONSHIPS OF THE HERMIT CRABS STUDIED

The species studied in this investigation were indentified by Dr. A. J. PROVENZANO, Jr., of the Marine Science Laboratory of the University of Miami. Specimens of the species studied have been deposited in the Museum of Comparative Zoölogy, Harvard University (MCZ numbers 12848 through 12858). These decapod crustaceans are members of the section Anomura. The systematic classification used in this paper is that proposed by MACDONALD, PIKE & WILLIAMSON (1957), based upon larval studies. This classification has been supported by further larval studies by a number of workers (PROVENZANO, pers. comm.).

The marine hermit crabs, characterized by poor calcification of the cephalothorax and the uncalcified, asymmetric abdomen, are divided into two families. The Diogenidae may be distinguished by the fact that the bases of the third pair of maxillipeds are close together and the chelipeds are either equal, or the left is larger than the right. In the Paguridae, the bases of the third maxillipeds are far apart and the right cheliped is usually longer than the left. The Diogenidae are more characteristic of shallow, tropical waters, while the Paguridae are more characteristic of deeper and colder waters. Important differences in larval morphology also separate the families.

Among the diogenid genera encountered in this study, the genera *Clibanarius* and *Calcinus* are more closely related to one another and distinct from *Paguristes*. Within the genus, *Clibanarius tricolor* and *antillensis* are more closely related to one another as are *Clibanarius cubensis* and *vittatus*.

The Paguridae includes among many other genera, *Pagurus* and *Pylopagurus*. *Pagurus miamensis* and *pygmaeus* are more closely related on morphological grounds than the other two species of this genus encountered in this study. MAKAROV (1938) mentions the possibility that a form similar to *Pylopagurus* may have given rise to the stone crabs, the Lithodidae. According to MACDONALD, PIKE & WILLIAMSON (1957) and others, the Lithodidae are derived from some pagurid form.

A taxonomic note which needs to be presented in the literature once again is the correct use of the generic names *Pagurus* and *Eupagurus*. As pointed out by PROVENZANO (1959) and others, opinions by the International Commission on Zoological Nomenclature have asserted the incorrectness of the use of *Eupagurus*. This name is a junior homonym of *Pagurus* Fabricius, 1775. Despite the mention of this situation in several articles, some workers continue to use the incorrect name *Eupagurus*.

SOCIAL BEHAVIOR OF HERMIT CRABS IN GENERAL

Before proceeding with descriptions of the social behavior of the species studied, it would be helpful to consider the repertoire of behavior patterns of a hermit crab.

The habit of inhabiting an empty gastropod shell markedly affects the behavior of hermit crabs. This is evident not only in certain special types of behavior (such as shell-fighting behavior) but even in modifications of their general locomotor behavior. Very few aspects of the behavior of pagurids are totally unaffected by the shell-carrying habit.

The behavioral interactions which two individuals can undergo may be divided into those in which sex is or is not an important factor. In this study, two important categories of behaviors of the latter type were observed: general aggressive behavior and shell-fighting behavior. Althought the sex of an individual may be of some importance in the general interactions of individuals and in shell-fighting behavior, it is not of major significance.

Most species of hermit crabs are gregarious to some degree. Some species live in distinct groups and repeatedly come in contact with other individuals of the group. When two individuals come so close to one another that they can sense each other by some modality and thereby effect a possible change in behavior (social contact), one of three types of behavior takes place. The individuals may show no change in behavior and thus appear to "ignore" each other (any externally unexpressed change in the organism's central nervous system, however important in later interactions, was by pragmatic necessity registered as "nothing" in the protocols of this study); if the sex of the organisms is appropriate and the individuals are in the appropriate physiological condition, sexual behavior may occur; the third possibility is aggressive behavior.

As in any animal, the aggressive interactions between crabs rarely reach a level of actual physical damage. Moreover, in hermit crabs, the gastropod shell protects individuals from conspecific individuals as well as predators. However, intense aggressive interactions can result in the loss of one or more limbs. Also, if for any reason an individual comes out of its "house", it will be attacked and eaten very quickly by its fellow crabs. In most cases aggressive interactions are on a symbolic level. Interacting individuals affect one another's behavior by movements and postures whose modes of action are as signals or displays, governed by evolved rules of communication. These behavioral exchanges can lead to physical attack and damage, retreat by one or both individuals, or apparent indifference. In this study of aggressive behavior patterns, simple tactile and visual stimuli were the only types investigated.

In the hermit crabs studied, the aggressive displays mainly involve positions and movements of the chelipeds or the ambulatory legs. In every species, the ambulatory legs (second and third pereiopods) may be moved rapidly away from the body in a characteristic fashion. This movement has been designated here as an

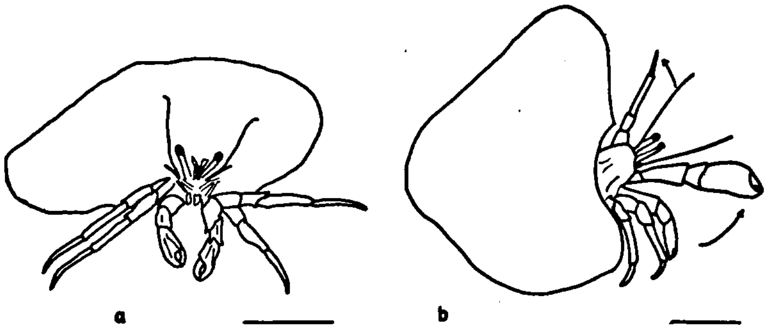
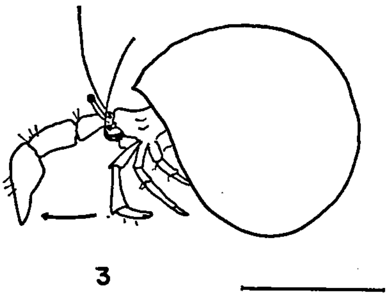


Fig. 2a. Single ambulatory raise, *Paguristes cadenati.* — 2b. Major cheliped extension and single ambulatory raise, *Calcinus tibicen* (Scale lines 5 mm)

ambulatory raise (see Fig. 2). The angle to which the limb is raised, the speed of movement and the relative positions of the limb segments vary from species to species, but the general pattern is the same in all species. The rigidity of the limb is variable, as it is moved from the normal (neutral) position (walking, climbing, standing, etc.) dorsally, through an arc of 30–75°, until the limb is at right angles to the body. There may be a minor forward component in the motion, depending on the species. Once raised, the limb may be held in that position for some time or be rapidly lowered. Incomplete lowering and movement upward to the fully extended position may occur. In addition to the single ambulatory raise, hermit crabs may raise both first walking legs simultaneously (double ambulatory raise) or may raise both first and second legs in a similar manner to effect a quadruple raise. In the latter case, the crab supports itself with its chelipeds. In all species, the first walking legs are used much more frequently than the second, and only rarely are one or both of the latter moved without movement of the former.

In some species, there are two rather distinct movements of the ambulatory legs: the ambulatory raise mentioned above and a second, forward directed movement which I have called the *ambulatory poke*. In this behavior the limb is moved away and up from the body. At the same time it is moved forward, and this forward movement continues as the limb is brought down. This behavior pattern usually appears to be directed toward the eyestalk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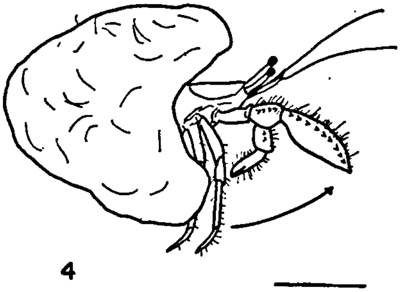
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Fig. 3. Major cheliped presentation, *Pagurus pygmaeus*.
Fig. 4. Major cheliped extension, *Pagurus marshi*. (Scale lines 5 mm)

region of the other crab. The limb often physically strikes the other crab.

Another group of movements that appear in aggressive interactions are those of the chelipeds. In some species it is possible to recognize two distinct types of movement-positions. I have called the first type of movement the *cheliped presentation* (Fig. 3). In this display, the crab lifts its whole body (and shell) slightly, spreads its legs a little and moves its cheliped forward until the dactyl is approximately perpendicular to the substratum. This position is more distinct in the genus *Pagurus*, where the chelipeds are normally held back under the mouth area. In these species there is a more pronounced movement of the chelipeds into the perpendicular, presentation position. The cheliped(s) and body are usually held in this attitude for some time unless the crab proceeds directly into a cheliped extension.

The *cheliped extension* is a movement that can act as a sign stimulus and also as a physically forceful movement. As will be shown later, it is a visually effective display; but it may also physically strike and move another crab. This movement has been described in *Calcinus laevimanus* (Reese, 1962b). The chelipeds move rapidly forward and upward until the limb is approximately parallel to the substratum (Fig. 2b and 4). When one crab backs into another, the chelipeds are frequently employed, pushing at the back of the shell. This is not always the stereotyped movement of an extension; sometimes an extension is attempted but can not be completed because of the obstruction of the alien shell. Moreover, in aggressive interactions two crabs may attempt extensions at the same time and result in pushing and hitting against each other's chelipeds. In both these instances, the chelipeds are not moved to the normal level for the species, due to the physical obstruction. In some pagurid species, it is not uncommon to see a smaller individual moved several centimeters when struck by the cheliped extension of a larger crab.

The movements described above were observed in all the species of hermit crabs studied (a possible exception is *Petrochirus diogenes*, which may not have an aggressive display involving the ambulatory legs). These movements of the ambulatory legs and chelipeds are rather stereotyped, although the physical orientation of the crab can effect minor changes in the movements. The level to which the limb is raised may vary somewhat depending on the intensity of the aggressive situation. However, these behavior patterns appear to be sign stimuli *sensu* TINBERGEN (1951). Tests described below have shown that these postures are effective stimuli. When individual crabs come into social contact (i.e. come close enough to effect changes in one another's behavior), these displays may be followed by retreat, apparent indifference (one crab may move over another which has just executed an ambulatory raise) or further aggressive interaction. Multi-action sequences of various behavior patterns often occur. As two individuals of equal size approach, both may raise their whole bodies slightly. Animal A may give a single ambulatory raise and animal B perform a double cheliped presentation. A then executes a double ambulatory raise, B a major cheliped extension, etc. until A and/or B retreat or crawl over the other. Interactions usually last only a few seconds, but long exchanges involving the execution of many aggressive displays, may last some minutes. General aggressive interactions can also develop into shell-fighting and occasionally into sexual behavior.

In addition to the general aggressive behavior outlined above, two other types of agonistic behavior patterns occur in hermit crabs. The first occurs as a distinct class of movements only in species in the Family Paguridae (the diogenid crab *Petrochirus diogenes* may be an exception). Individual crabs often crawl onto the top of the shell of another crab. If the size relationship of the crabs is within certain limits, the crab crawled upon may move up and down and/or side to side rapidly. This motion may cause the other crab to fall off. This *dislodging-shaking* behavior pattern will be discussed more fully under *Pagurus miamensis.*

Shell-fighting behavior was observed in all the hermit crabs studied. This behavior is peculiar to hermit crabs. As hermit crabs grow they must periodically obtain a larger gastropod shell to inhabit. If no empty shell is found, the crab may attempt to get a more suitable shell that is already occupied by another hermit crab (usually conspecific although interspecific fights do occur).

If the defending crab does not duck back into its shell at the approach of the attacking crab, an aggressive interaction may take place. After the defending crab has ducked in, the attacker turns the shell over several times, holding it with its ambulatory legs. It then places its cheliped(s) into the aperture of the shell. During this latter investigation and the subsequent behavior patterns, the crabs are in what I have called *"opposed"* position. If both crabs were in their normal position in the shell, they would have their eyestalk-mouth areas and ventral cephalothorax surfaces opposite one another. However, one crab is usually withdrawn into its shell, thus obscuring whatever it may be doing. The other crab holds the shell with its ambulatories around the aperture of the shell. In this attitude, with apertures facing each other, the attacking crab is in a position to easily place its chelipeds in the hole of the other crab's shell.

In all species, the aggressor next goes through *positioning* behavior. In general form, this consists of the attacker moving from side to side, over and slightly below the aperture of the defender's shell, while the defending crab's shell remains stationary. This movement of the whole body and shell, with the ambulatory

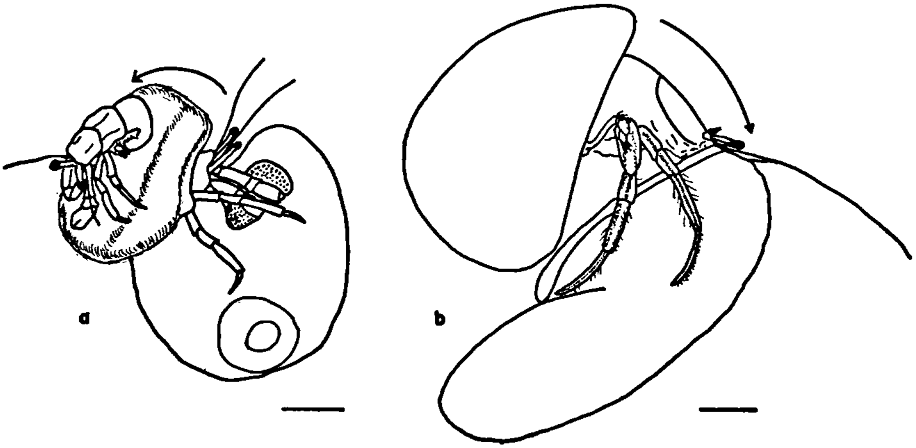
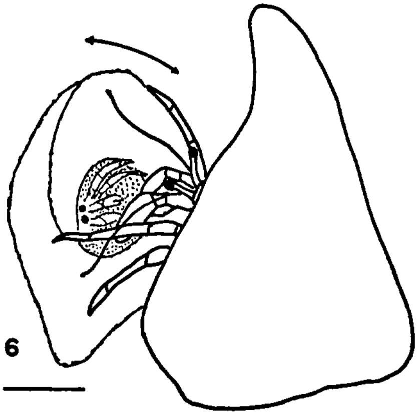


Fig. 5a. Shell-fight, *Calcinus tibicen*. Loser "nude" on back of shell of winning crab. (Scale line 5 mm) — 5b. Shell-fighting, rapping in *Clibanarius cubensis*. Shell of attacker in raised position. (Scale line 10 mm)

legs held stationary, describes a horizontal figure 8 in most species. The movements of the aggressive crab often cause some movement of the shell of the defending crab. The attacker then proceeds directly into *rapping* behavior (Fig. 5b). This is the most striking portion of this behavior pattern. In the diogenid hermit crabs, the attacker hold its ambulatories and cephalothorax stationary while through a movement of the abdomen, the aggressor's shell is rapidly brought forward into contact with the defender's shell. This physical striking can produce a click clearly audible to an observer. It was this clicking that initially attracted my attention to a pair of *Clibanarius tricolor* which was engaged in a shell-fight. The pattern is quite different in pagurid crabs although the movement of the interacting pair appears similar. The majority of the rapping is effected by the attacker moving the defender's shell back and forth through motion of its own ambulatory legs. The attacker's body and shell usually remain stationary while the defender is moved roughly parallel to the anterior-posterior axis of the attacker. These crabs also perform rapping of the diogenid type, but the effective behavior is the very short rapid *spasmodic shaking* characteristic of the Paguridae.

Observations of crabs in clear plastic shells and of the exit of the losers in normal fights, have strongly indicated that these movements are not simply the application of physical force by the attacker. Although the chelipeds of the attacker are often placed into the shell aperture and the first or both pairs of ambulatories may also be placed down the aperture, little or no physical contact between the appendages of the two crabs takes place. After a varying number of raps, the defender may come forward, move out of its shell completely, and climb onto the back of its own or the attacker's shell (Fig. 5a). With its chelipeds and ambulatories, the attacker usually examines the now empty shell, and then very quickly shifts from its former shell to the recently vacated one. As the crab places its abdomen and cephalothorax into the new shell, the chelipeds and ambulatories are rapidly shifted to hold onto its former shell. The crab may hold the old shell for some seconds as it moves up and down within the new shell and may eventually switch back to the old one. The winning crab always "tries out" the shell it has won, although it may abandon it after moving about within (while holding the old shell). However, it usually releases its hold on the old shell after several seconds. The defeated crab then quickly gets into the empty shell. If the loser does not stay close to the shells in question, and move into whichever one the winning crab leaves empty, it is almost always killed by conspecific individuals if not by some other organism. Empty shells are rare and a naked crab has little chance of finding one of habitable size before it is eaten.

The other class of behavior observed was sexual behavior. However, the patterns associated with mating are best described according to species. Certain generalities are possible and species' similarities and differences are very interesting. Very briefly, just before a female crab is ready to mate (shortly before moulting) she may come in contact with a male. In some species, the male carries the pre-moult female about for many hours before initiating specific precopulatory behavior. If the female possesses any matured larvae from a previous mating, she releases them and moults (the sequence is different in *Pagurus bonairensis* and *Paguristes cadenati*).



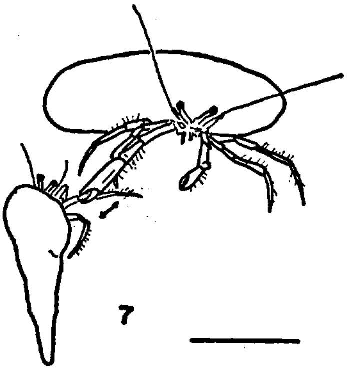
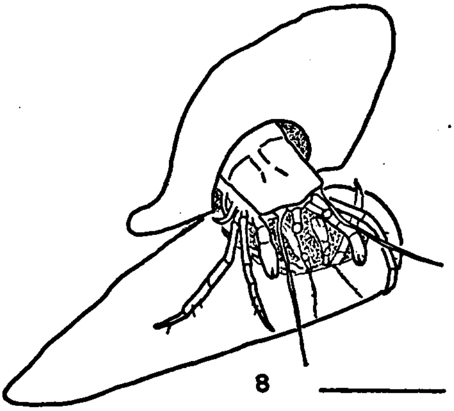


Fig. 6. Precopulatory behavior, *Calcinus tibicen*; male rotating female.
Fig. 7. Precopulatory behavior, *Pagurus bonairensis*; male (on right) jerking female back and forth. (Scale lines 5 mm)

Prior to and usually continuing shortly after female moulting, the male performs certain precopulatory behavior patterns. These vary widely, but the most common are rotating-shaking the female (Diogenidae; see Fig. 6) and jerking the female toward the male by short movements of the male cheliped (Paguridae; see Fig. 7). After some minutes or hours of the appropriate behavior patterns by the male, the female signals the male by movements of her chelipeds in his mouth region (see Fig. 8). The male then eases out until most of his cephalothorax is out of the shell (Fig. 9). The female also moves out of her shell and the ventral surfaces are opposed as the male's fifth pereiopods move spermatophores from the genital openings at the base of his fifth pereiopods to the region of the female genital openings, at the base of her third pereiopods. Both crabs then rapidly pull back into their shells and a variable period of postcopulatory behavior by the male follows. In some species there may be more than one copulation by the pair. In others, the male performs postcopulatory behavior until the female has the new set of eggs in place on her pleopods.



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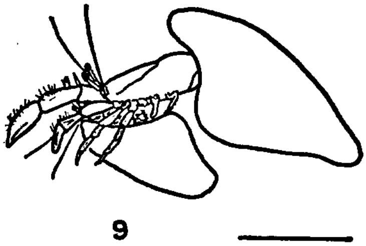

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Fig. 8. Precopulatory behavior, *Clibanarius antillensis*; female tapping male below eyestalks just prior to easing out for copulation.
Fig. 9. Copulation, *Pagurus miamensis*; female obscured by male. (Scale lines 5 mm)

DESCRIPTIONS OF BEHAVIOR PATTERNS

Clibanarius tricolor (Gibbes, 1850)

(Family Diogenidae)

This species is discussed first, because of the more extensive investigation of its behavior. Descriptions of the methods used for most measurements will be given in this section but not repeated for the other species.

This small active crab is certainly the most abundant and widespread hermit crab in the waters aroung Curaçao. Its abundance makes the fact that it has not been reported from the island seem unusual. The blue, orange and yellow banded ambulatory legs are strikingly colored; as with most species, the walking legs are almost all that an observer sees in the field. It is a small crab, large males attaining a cephalothorax length (c.l.) of only ten millimeters. Most individuals are less than five mm in c.l. Ovigerous females with cephaloth orax lenghts of 2.5 mm have been collected. Males are generally larger than females, as was true with all the hermit crabs studied. Other than general size there is no visible external sexual dimorphism. BUSH (1930) and PEREZ (1932) have reported minor sexual differences in two European species of hermits, but these would be difficult to use for sex identification in the field.

Populations of *Clibanarius tricolor* were found in most of the areas inhabited by marine hermit crabs. It was very abundant in shallow waters, along open shores on both the north and south coast of Curaçao. It was not found below the very rough, surf-punded cliffs on the north shore, but was in tide pools filled by spray from the breakers. It was reasonably numberous in those bocas and bays where the surf action was reduced. It was rarely located below three meters of water and was most abundant in one meter or less. In addition to open water, rock-covered areas *tricolor* was present in the entrances to bays such as Piscadera Baai and St. Martha Baai. It was also found, although not abundant, on some of the mudflats of Piscadera Baai and Spaanse Water, but appeared to be absent from many of the mudflats near Brakkeput.

The microdistribution of individual groups varied according to local ecological conditions. In all areas this species is nocturnal. During the day the crabs move about slowly or rest. Feeding activity begins at dusk and continues throughout the night. In certain areas, the members of a population are very contagiously distributed during the day. A gentle slope, rocky bottom and open circulation seem to be conditions that facilitate the formation of these dense aggregations. The crabs congregate among small rocks in about 30 centimeters of water. In areas where the water circulation was not as good (such as inside Piscadera Baai) or the bottom contained large rather than small, detritus-covered rocks (north shore bocas), the crabs never formed the very dense groups such as were found in front of Carmabi, outside St. Martha Baai and on the shallow shelf of Boca St. Michiel.

In some areas, the number of individuals was systematically counted. A half-meter square was used to mark off quadrates and all hermit crabs present in each quadrate were counted. In some cases, the sampling was carried out along a line, parallel to shore, since *Clibanarius tricolor* was absent elsewhere. Usually an area was chosen which included a concentration of crabs, but the limits of the total area measured were defined largely by the author's fortitude. In some cases, the crabs in a quadrate were collected and later counted in the laboratory. The distributions were then tested statistically for non-randomness. The index of dispersion, I_δ, introduced by Morisita (1959), was used. If this index is equal to 1.00 the individuals within the sample are randomly distributed. If I_δ is greater than 1.00 the distribution is contagious. Morisita also gave a formula for calculating an F_0 value to determine the statistical significance of the I_δ. Tables 1 and 2 give the results, for *C. tricolor*, of the measurements taken in different areas. It can be seen that in all cases, the I_δ value for the distribution is much above 1.00 and the F_0 value shows that the value is statistically

TABLE 1

FIELD DISTRIBUTIONS OF *Clibanarius tricolor*

Boca St. Michiel

n	f	nf
0	13	0
26	1	26
83	1	83

$q = 15$ $N = 109$
$I_\delta = 9.49$
$F_0 = 66.50$

Spaanse Water

n	f	nf
0	21	0
1	2	2
9	1	9

$q = 24$ $N = 11$
$I_\delta = 15.70$
$F_0 = 7.39$

St. Martha

n	f	nf
0	1	0
2	1	2
4	1	4
9	1	9
10	1	10
11	1	11
12	1	12
13	1	13
14	1	14
18	1	18
51	1	51
150	1	150
200	1	200
650	1	650
2336	1	2336

$q = 15$ $N = 3480$
$I_\delta = 1{,}705.20$
$F_0 = 423{,}000 +$

n is the number of individuals in one quadrat
f is the number of quadrats with n number of individuals
q is the total number of quadrats
N is the total number of individuals
I_δ is the index of dispersion; $I_\delta > 1.00$ indicates a contagious distribution
F_0 is the F value measurement of the statistical significance of the I_δ value

very significant ($p \leq .01$) in all cases. In some cases, such as St. Martha ($I_\delta = 1{,}705.20$) and Carmabi #2 ($I_\delta = 2{,}865.81$) the F_0 value was not fully calculated. A total of 53.5 square meters was sampled. The density of *tricolor* in the areas sampled ranged from 0 to 928 specimens/square meters.

A field count taken early in the summer of 1962 could not be listed with the other measurements due to the method used. In this measurement, a group of *Clibanarius tricolor* was collected and counted. The group occupied an area 10 cm wide and 30 cm

TABLE 2

FIELD DISTRIBUTIONS OF *Clibanarius tricolor*

Carmabi			Piscadera Baai Channel		
n	f	nf	n	f	nf *
0	32	0	0	43	0
1	5	5	1	27	27
2	5	10	2	22	44
4	1	4	3	19	57
5	2	10	4–6	17	83
6	1	6	7–9	10	75
10	3	30	10–12	13	135
12	1	12	13–15	6	85
15	2	30	16–19	13	239
20	1	20	20–26	10	231
25	2	50	27–36	23	716
31	1	31	38–48	9	378
40	2	80	49–55	8	402
45	1	45	62–83	9	615
60	1	60	92	1	92
100	2	200	93	1	93
2,654	1	2,654	100	2	200
3,512	1	3,512	104	1	104
			175	2	250
			210	1	210

Carmabi:
$q = 64$ $N = 6{,}759$
$I_\delta = 2{,}865.81$
$F_0 = 300{,}000 +$

Piscadera Baai Channel:
$q = 237$ $N = 4{,}040$
$I_\delta = 3.84$
$F_0 = 49.60$

* Data presented grouped here, although I_δ and F_0 were calculated on un-grouped data.

long. In the surrounding 16 square meters there were 175 individuals of *tricolor*. In the group, there were 3,697 *tricolor*, five empty gastropod shells and no other species of hermit crabs. This distribution corresponds, in order of magnitude, with the dense aggregations at St. Martha and Carmabi. In all the measurements of field distributions, the index of dispersion indicates that this species' distribution is strongly contagious. In the very dense aggregations, individuals are often congregated four, five or more deep on top of one another.

These aggregations of *Clibanarius tricolor* are usually formed in relatively open areas, spread over several of the medium-small rocks which cover the bottom. Several aggregations were located at least partially beneath the overhang of large rocks. The individuals concentrated in these groups were mostly small and medium size individuals of less than 4.0 mm c.l. Larger individuals, mostly males, were present about the perimeter of the aggregation and adjacent area. At about 16.00 hrs, the crabs in the aggregation began moving about within the limits of the group. When a crab came to the edge of the group, it turned and moved back into the group. But by 16.30 hrs, the top layers of the aggregation were moving out in the direction of the nocturnal feeding area. And by 17.00 hrs all individuals had left the area of the diurnal aggregation and dispersed over the surrounding rocks for several square meters.

Members of a group all move in one general direction. In one section of the shallow waters in front of Carmabi, there were several aggregations just a few meters from one another. In the evening, members of one group moved into deeper water, almost directly southwest. They eventually spread out over a semicircular-oval area about four meters in diameter, SW from the location of the diurnal aggregation location. The second aggregation in the area mentioned also started moving out at 16.30 hrs and fed during the evening and night. However, they moved parallel to and slightly toward the shore, i.e. west and west-northwest. As the crabs move outward and throughout the night, they move their chelipeds up and down, from the substrate to their mouth regions, picking at the detritus-covered rocks on the bottom.

A pilot experiment was carried out with these aggregations to measure group stability. Several hundred individuals of one group were removed, dried and marked on the shell with red ink and several hundred of the other group were marked with blue ink. These crabs were replaced in their respective groups and daily counts were made thereafter. The ink used did not last for very many days. (During the day, crabs frequently pick at the surface of the shells of other individuals with their chelipeds.) However, the observations for the first few days revealed relative group stability, although there were some blue-marked crabs found in the red group and vice-versa. However, the majority (82%) of the marked individuals observed remained in their "own" aggregation day after day.

An effort was also made to gain an idea about the spatial stability of these groups. The locations of three aggregations were determined in relation to large rocks in the immediate microenvironment. The group locations were noted on March 15, 1963 and every day thereafter until March 25. The observations were carried out at 11.00 hrs every day. The groups were 10–20 cm long and 5–10 cm wide. On the 16th of March all three groups were in exactly the same location but exhibited minor changes in general shape. On the 17th, the first two groups were the same but the third had shifted 120 cm westward. By the 18th, the latter had split into two subgroups and no definitive group could be found. The first two groups maintained themselves as to numbers but had shifted about 10 cm toward the shore during the 10 days of observation. Their shapes did change slightly from day to day.

On April 22 one of the groups was chosen and after the aggregation had emigrated in the evening, the largest stone upon which the crabs had been partially grouped for the previous two days, was moved 10 cm toward shore. When the group was reformed on April 23, it was in the same location. The crabs were on the exposed sand where the large rock had been. No crabs were on the rock that previously was covered with several hundred individuals. Chemical orientation experiments described in a later section, indicate that individuals of *Clibanarius tricolor* orient strongly toward conspecific individuals. It is possible that the exact location of aggregation formation is determined initially by movement to a limited general area, then more specifically to the presence of conspecific individuals in the area.

The crabs feed during most of the night. About 04.00 hrs they start moving directly toward the area of aggregation. As individuals get closer to the formation area, they move more rapidly until in the area. By 04.30 large numbers of the crabs are in the area and by 05.00 the aggregation is formed. The animals move about within the group for some minutes but soon become quiescent.

Observations of the daily timing of the movements were carried out on a number of days throughout my period of study in Curaçao. The evening movement occurred at the same time every day. This was true whether the sun had been out continually (usual condition), intermittently or the day was continually overcast or even rainy all day. The latter climatic condition occurred once during the 10 months during 1962–63 I was in Curaçao. Three aggregations of *Clibanarius tricolor* were checked that day and all emigrated at the usual time. At this time of day, the sun is at an angle of about 35° above the horizon. At the beginning of the morning return movement there is no visible sunlight. By the time the group is reformed there is some light, but the sun itself is not visible.

I was interested to learn what sort of dispersal patterns would be formed under more uniform conditions, such as could be established in the laboratory. Supplied with fresh running seawater, hermit crabs adapt well to laboratory conditions. As far as could be judged, their behavior in the laboratory and field were qualitatively the same. One behavior which was not fully manifested in the laboratory however, was the formation of dense groups. As seen below, the crabs did aggregate. But even under the most natural conditions established in the laboratory, the formation and daily dispersal of aggregations did not clearly occur. The first attempt to measure dispersion under more uniform conditions was carried out using small rectangular glass aquaria (21 by 35 cm). The bottoms were evenly covered with fresh clean sand and the lighting was by overhead lights about two meters above the level of the tanks. The natural light cycle was not altered. Counts of the individuals in 15 quadrates, 7 × 7 cm were taken at various hours on two different populations established from portions of aggregations collected in front of Carmabi. The results of these counts are given in Table 3, along with the I_δ and F_0 values for each distribution. As can be seen, especially in population #1, there was a tendency to group in the corners and along the edges of the tank. In order to avoid this tendency and present a more uniform environment in which the crabs could disperse, a circular container (38 cm in diameter) was used. Fresh sea water was introduced into the center of the container. A uniform sand bottom was present. The top of the container was divided into 32 equal segments by radii. Counts were made of the individuals of three populations established in this container. The results for one experimental population are presented in the histograms of Figure 10. As can be seen, the crabs were distributed contagiously in all cases. Three additional counts of the dispersal of the other populations gave similar results (average $I_\delta = 1.37$, $F_0 = 6.89$). These results indicate that *Clibanarius tricolor* is gregarious in its distribution since they group contagiously even in a uniform environment.

In addition to the previously mentioned marking experiments, some pilot studies on individual daily movements were made. There are populations of *Clibanarius*

TABLE 3

LABORATORY DISPERSAL OF *Clibanarius tricolor*

Laboratory population #1:

08.30 hrs. July 10

60	34	16	17	43
35	9	9	14	20
53	16	18	25	56

$I_\delta = 1.320$
$F_0 = 10.64$
$p < .01$

16.00 hrs. July 10

16	10	2	8	19
21	9	6	8	52
33	10	23	59	103

$I_\delta = 1.904$
$F_0 = 25.28$
$p < .01$

00.00 hrs. July 11

53	25	25	42	73
33	15	16	28	32
33	17	23	39	61

$I_\delta = 1.198$
$F_0 = 8.26$
$p < .01$

16.00 hrs. July 11

46	23	46	23	46
40	70	5	41	48
17	20	9	33	98

$I_\delta = 1.35$
$F_0 = 15.07$
$p < .01$

Laboratory Population #2:

00.00 hrs. July 11

6	25	22	17	19
19	69	27	14	14
19	43	62	45	29

$I_\delta = 1.335$
$F_0 = 11.28$
$p < .01$

16.00 hrs. July 11

20	23	21	16	16
10	50	35	7	5
23	30	36	14	14

$I_\delta = 1.26$
$F_0 = 6.92$
$p < .01$

12.00 hrs. July 12

11	13	25	5	17
16	75	29	5	4
18	23	44	50	51

$I_\delta = 1.56$
$F_0 = 16.42$
$p < .01$

13.00 hrs. July 13

15	22	18	19	17
17	102	16	20	22
27	21	22	43	39

$I_\delta = 1.54$
$F_0 = 17.74$
$p < .01$

tricolor along the east shore of the entrance to Piscadera Baai. The bottom drops quickly to about three meters after a shallow shelf about 50 cm wide and *tricolor* is found mainly on this shelf. In three separate experiments, a total of 65 individuals was marked and placed back in the water. In each experiment the area was searched

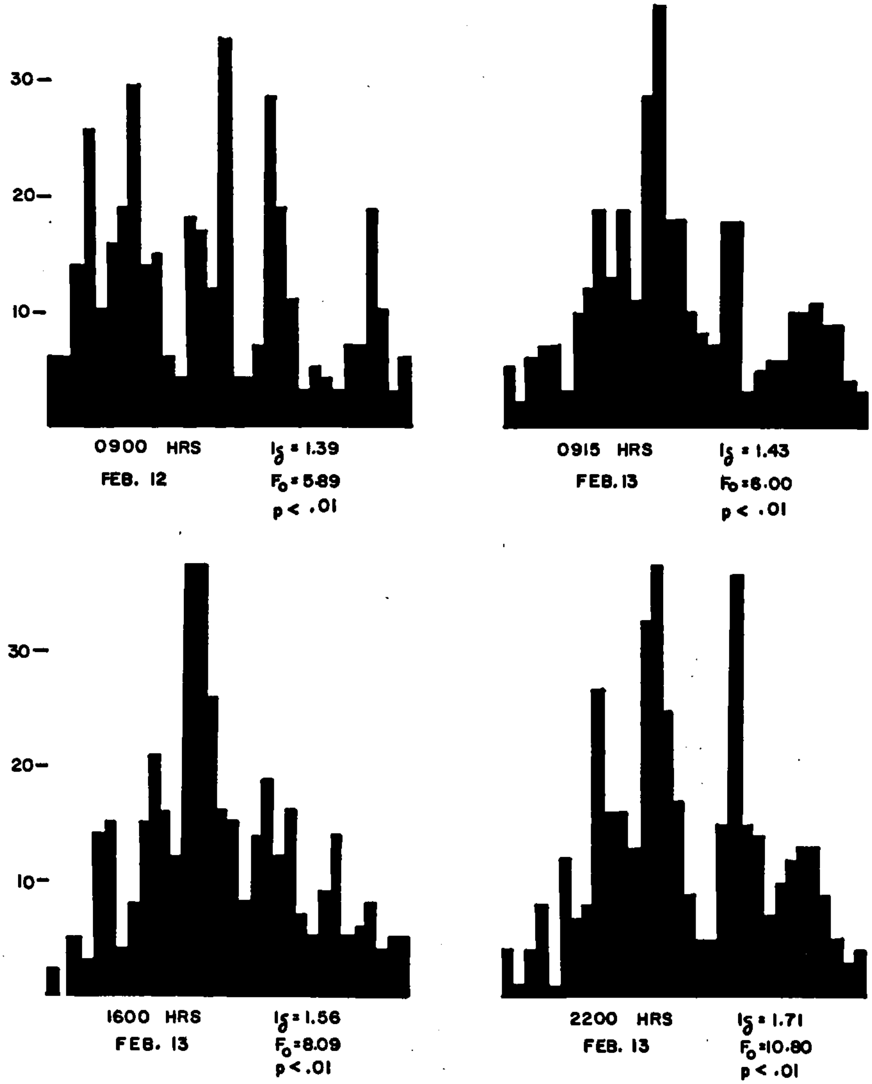


Fig. 10. Laboratory distribution of *Clibanarius tricolor*. Histograms of number of individuals found in 32 equal segments of circular container.

for marked crabs for 5–12 days after marking and release. As in other field marking experiments, recovery of marked individuals was not high. Figure 11 shows the distances which marked crabs moved from day to day. All measurements were made around 12.00 hrs. A total of 80 individual daily movements were measured. The mode of the results is the 0–20 cm movement group with 16 instances. The next largest is the four meter group with ten cases. The greatest distance recorded for a crab's movement in one day was ten meters.

Clibanarius tricolor is neither a rapidly nor slowly moving crab relative to other species. As in most hermit crabs, the gastropod shell is dragged along on the substrate. Although surprisingly agile for an organism carrying so much extraneous weight, individuals often tumble over backwards when attempting to crawl over an obstacle and lose their hold on it. They are usually able to right themselves rapidly through movements of their second ambulatories. All walking and crawling movements are carried out by the ambulatory legs – the second and third pereiopods. The chelipeds in this species are small and weak and rarely used for support. In feeding,

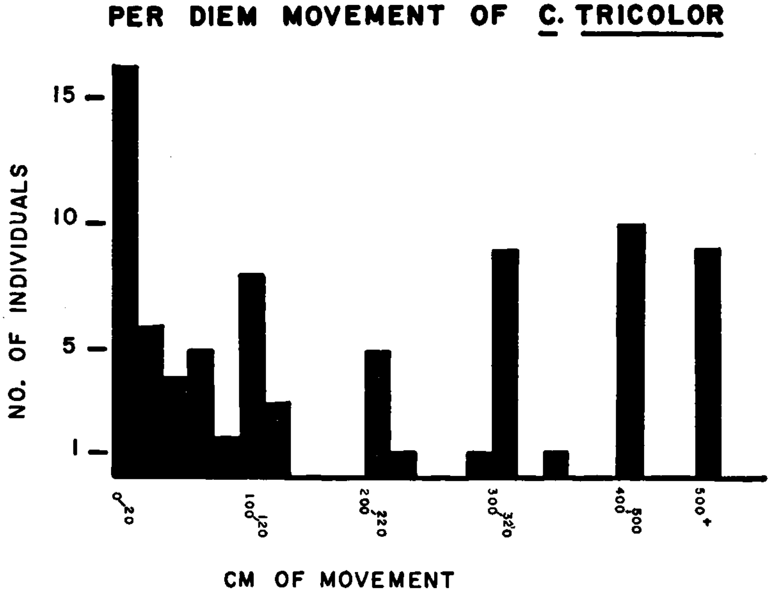


Fig. 11. Daily movement of *Clibanarius tricolor*. Distances moved in 24 hours by individual crabs.

the chelipeds are used alternately, picking up bits of detritus matter or occasionally larger food (fellow hermit crabs, dead fish or molluscs). *Clibanarius tricolor* has in its behavioral repertoire, most of the behaviors mentioned in the introduction to this section although some are not strongly expressed. When two individuals come into contact, they often show no change in their behavior, and one may crawl over the other or they may pass one another without any apparent notice or contact. Even when aggressive movements are made by one crab, the other frequently shows no change in behavior. Such a manner of interaction is logical in a species that lives in such continual intra-specific contact.

When two crabs come in contact, the most frequently used aggressive signal is the single ambulatory raise. The movement can be executed by the crab when it is on level substratum or while crawling about on objects in its environment. When walking in a normal manner, the ambulatory legs are held at an angle of about 25° from the dorso-ventral plane of the animal. The ambulatory raise is executed with the limb held rigid and straight. Moving through about 60°, the limb is brought almost perpendicular to the dorso-ventral axis. However, the leg is rarely raised to a completely perpendicular position. In the raised attitude, the distal segment is very slightly inclined downwardly. The upward motion takes from 0.18–0.24 seconds (all speeds measured from motion picture films). Once in the raised position, the leg may be immediately lowered (i.e. no frames of film in which the limb is clearly maintained in the extended position), held in place for a short time or be held in place for some seconds. This maintaining of a sustained raise was rather common during aggressive interactions between crabs of equal size. The downward movement is not as stereotyped as the upward motion. The limb is not always maintained in a rigid manner and the distal segments may be moved before the more proximal. The speed of movement is highly variable. The leg may be brought down rapidly (0.24 seconds), but the process is usually slow (over 0.5 seconds). A second raise may be executed without returning the limb to the neutral resting position. The forward component of the ambulatory raise is slight in *Clibanarius tricolor.*

Both of the second pereiopods may be raised as described for the single raise. Usually both are lifted simultaneously. However, occasionally the movement of one limb is started before that of the other. This asynchrony occurs more often when the execution of a double raise quickly follows a single ambulatory raise and the limb involved in the latter behavior is not returned completely. In more intense aggressive interactions, individuals of *tricolor* may employ all four ambulatory legs in a quadruple raise. While all four legs are engaged in this manner, the animal maintains an upright position by using its chelipeds for support and/or leaning back, balancing itself on its shell. The posterior legs are not raised as fully as the second pereiopods. They usually are not lifted above 75° from the dorsal-ventral axis.

The cheliped extension behavior pattern is not strongly developed as a symbolic aggressive movement in *Clibanarius tricolor.* Often this movement of the chelipeds is interrupted in its motion by striking against the shell of another crab. Although the behavior pattern appears to have communicative value, its execution, as to speed and position, is variable. The chelipeds may be raised rapidly or rather slowly to various positions between perpendicular to (resting position) and parallel to the substratum. However, quite frequently, a crab does execute a rapid movement (less than 0.5 seconds), bringing one or both of its chelipeds through about 80° arc to a position slightly below parallel to the substratum. On a few occasions, I observed individuals, leaning back on their shells, execute a sustained quadruple ambulatory raise and a double cheliped extension at the same time.

As mentioned above, the behavior of one individual may appear unchanged by social contact with a conspecific, even when one organism executes an aggressive movement. However, the performance of an aggressive movement usually is immediately followed by (1) an aggressive movement by the other crab, (2) some form of retreat by the other crab of (3) further aggression or retreat by the original individual. Long series of aggressive exchanges do occur and equally matched pairs may interact for some minutes. In long series, the most common situation is that the two crabs, facing one another about five mm apart, both execute sustained single or double ambulatory raises, holding the limbs in the raised position for many seconds. Often, one crab reverses or alters its direction of movement, clearly in response to the approach of another crab, before any aggressive movements are made. In addition to backing away and/or changing its direction of forward movement, a "retreating" crab may duck back inside its shell. Sometimes the other crab will turn the shell of a retreating crab over on its back. It may examine the hole of the shell with its ambulatories and chelipeds or pass on once it has turned the shell on its back. This behavior was more frequently executed following a long interaction in which one crab finally retreated, moved back and was then grasped by the ambulatories of the other crab and turned over. An individual which has been on its back, either by accident of the actions of another crab, always comes to the entrance of its shell aperture in the same position. The chelipeds are held at an angle of about 45° to the anterior-posterior axis. The ambulatory legs are held very close together at first , but as the crab comes out of the shell they separate slightly. Both pairs of legs are widely spread, approximately in the position of a quadruple ambulatory raise. The crab may maintain this posture for several seconds before righting itself through movements of its ambulatories.

Clibanarius tricolor was the first species in which I observed shell-fighting behavior.

As the attacking crab approaches another, an exchange of aggressive movements may take place or the other crab may retreat right away. An attacking crab often moves into contact from behind and turns the other on its back. After moving into an "opposed" position – with apertures directly opposity one another – the attacker may then turn the crab and shell over several times through 360° by movements of the ambulatories. Some investigation of the shell aperture and interior by movements of inserted chelipeds and ambulatories may then occur. With the walking legs spread on the outside around the edge of the aperture, approximately forming a horizontal X, the attacker goes through "positioning" behavior. This behavior pattern is relatively brief in *C. tricolor*. The body and shell of the attacker move in a horizontal figure 8, with the ambulatories remaining stationary on the defending crab's shell. The motion may be strong enough to rock the defending shell from side to side on the substrate. Each cycle of movement takes about one second and usually 3–5 cycles are executed before rapping begins. Initially, rapping is always carried out with all four legs outside but in prolonged fights, one, two or all ambulatories may be inserted inside the hole of the defending crab's shell. In rapping, the ambulatories and cephalothorax remain approximately stationary as the attacker's shell is raised until about half of the cephalothorax is exposed. The shell is then brought down rapidly. The downward motion brings the upper edge of the shell very close to the upper edge of the defending crab's shell. The area of the first whorl of the shell just below the rim of the aperture of the attacking crab comes in contact with the corresponding position of the defending crab's shell. This contact appears to produce the sounds sometimes heard accompanying the rapping motions. The motion is somewhat circular when viewed from the side, moving about 30° through an axis running parallel to the surface of the shell apertures and located near the lowest portion of the first whorl of the shell of the attacking crab. The complete cycle of movement from up, to down and back up averaged 0.33 seconds in duration. The range for complete cycles, measured from films, was 0.18–0.62 seconds. The exact speed of downward motion could not be measured since the complete action occurred in less than 0.06 seconds, the shortest period of time measureable with the films taken. The movement from the down position to the raised attitude was 3 to 5 times as long as the downward motion, taking between 0.18 and 0.30 seconds. The attacking crab always began its downward motion as quickly as the shell was fully raised. The time the crab remained in the fully down position was variable.

An attacking crab may rap just once, but more frequently, it carries out a series of rapping movements. The series may vary from a few to 20 to 30. The later raps in a series almost always are weaker and move through a shorter distance. In addition, a series of raps may all be weak short movements of less than 1/4 the length of the cephalothorax of the crab. After a series of rapping movements, a crab may go into the aperture of the defending crab "head-first". The two shells are closely pulled together and neither crab can be seen. This position may be maintained for minutes without any visible motion. More rapping may begin directly from this position, but more frequently, the attacker comes out and begins rapping either after or without positioning behavior. Between series of rapping movements, the attacker frequently moves its chelipeds up and down alternately in the shell aperture without going into the hole. A crab can begin a series of raps with all legs outside and one by one move all ambulatories into the aperture with very little interruption in rapping. Although rapping always follows positioning behavior, the latter is not a necessary prerequisite for the former and cheliped movements may or may not precede rapping or positioning.

A complete shell fight, successful or unsuccessful, may consist of a minimum of positioning followed by one short series of rapping motions. Conversely, some unsuccessful attackers may "fight" for a number of minutes and execute over 100 raps before releasing the other crab. When it does give up, an attacker almost always leaves the defending crab on its back and as the defender tries to right itself, it may again be attacked. Occasionally, after a sequence of shell-fighting interaction, the defending crab will come up and, by a series of aggressive movements, cause the attacking crab to retreat.

The last behavior of a successful attack invariably is rapping. After "sufficient" stimulation, the defending crab starts moving up to the entrance of its shell aperture. As this happens the attacking crab moves back away from the defender and from a slightly lower position, carries out a few more raps. As the defending crab moves out of its shell completely, the chelipeds of the attacking crab usually rest on the lower lip of the aperture. Occasionally they appear to be in contact with some part of the losing crab and may actually exert some physical force to hasten or assure the exit of the loser. However, in the majority of fights, no such physical pulling or tugging was observed. After the loser is "extracted", the winning crab usually investigated the interior of the shell briefly with its chelipeds and ambulatories while the nude loser moved about on the back of the shell of the attacker or its own shell. In crowded conditions, such as are common in nature for this species, the loser is subject to almost certain death from the attacks of conspecific individuals if the winner prevents its entering a shell for more than a few seconds. A naked crab can not protect its abdomen statisfactorily and is torn to bits rapidly.

After initial investigation, the attacker usually then moves into the new shell. As it moves, abdomen first, from one shell to the other, it quickly moves its ambulatories from the shell it is moving into to the shell it has just occupied. It does this in such a manner that it maintains possession of both shells even after it has moved into the new one. The winning crab frequently backs all the way into the new shell (as far as its hold on the old shell will allow), presumably testing the fitness of the new shell. It may change back to the old shell, but normally once won, a new shell is quickly occupied and the losing crab moves into the old shell of the winning crab. On one occasion I observed a successful fight, complete with double shell change, followed immediately by a second fight between the same two crabs. The winner of the first fight was again victorious and won back the shell he had just vacated.

As in many crustaceans, mating in *Clibanarius tricolor* apparently can be successfully only for a short time following a female moult. Some time prior to her moulting, a female is grasped by a male. This time may vary from a few minutes to five, six or more hours. (Six hours was the longest period of time a mating pair was observed prior to copulation. Longer pairings probably do occur). A male may grasp a premoult female and after moving the shell around to an opposed position, may hold it quietly for some minutes. More often the male moves one or both chelipeds down into the aperture of the female and moves them up and down. These movements of the chelipeds occur periodically throughout precopulatory activity. The male may then carry out a few rocking movements. These movements are of two types in *tricolor* and are the most consistant and conspicuous elements of mating behavior. The male holds the female with his ambulatories in a wide X around the aperture of the female. The body of the male is not directly over the female but the mouth region is over the lower lip of her aperture. The male holds its chelipeds just at the entrance of the shell aperture. In this position, with the female below and slightly in front of the male, the male moves the female back and forth around an axis running through and perpendicular to the plane of her aperture. Initially the male always performs a "gentle" rocking movement in which the motion is very slight, the movement of the male ambulatories not exceeding the length of a *tricolor* eyestalk (less than one mm). The rocking is carried out in series of three to six or more cycles at the rate of two to three per second. The apex of the female shell only moves through about 10° arc during this rocking. Series of gentle rockings may be interspersed with quiet maintenance of position or an alternating movement of the chelipeds up and down in the aperture of the female. Occasionally the male will push the female back and forth about an axis parallel to the columella axis of the female. This may either precede or follow rocking movements.

At first occasionally, and later more frequently, the gentle rocking is interspersed with "violent" rocking by the male. This is also effected by movement of the male ambulatories, but is more rapid (0.18 seconds/cycle) and the female is moved through a greater distance (40–45° arc). The movement is not purely circular but approximately in a horizontal figure 8. That is, the tips of the male ambulatories move asychronously in ovals rather than in simple arcs. This rocking-shaking may proceed with the female shell on the substratum or the male may lift the shell entirely off of the substrate and rock the female about in the water. The latter can only be done when the male is substantially larger than the female. Males of mating pairs averaged 47% larger (c.l.) than females; the range for the pairs measured was 20–70%. The violent rocking behavior is also carried out in short series of 3–6 cycles.

Violent rocking is usually followed by gentle rocking and/or cheliped movements by the male. As this precopulatory activity proceeds, the female may occasionally come to the surface of her shell aperture only to retreat again following cheliped movements by the male. Several hours before copulation, the male may begin violent rocking and the frequency of occurrence of all behaviors gradually increases. Shortly before copulation, the female moults.

(Non-virgin females usually release the larvae from previous matings before they are grasped by a male. I did find a few males performing early precopulatory behavior with females which were still carrying a matured brood.) When the female moults, the male grabs at the old exoskeleton of the female and pulls it out of the shell. On several occasions the male actually "helped" the female out of her exoskeleton by actively pulling at the legs and chelipeds. After helping the female out of her old exoskeleton, the male moves his chelipeds up and down in the aperture of the female. After a series of either type of rocking or cheliped movements, the female comes toward the rim of her shell aperture and as she eases out, she moves her chelipeds and antennules rapidly in the mouth-eyestalk region of the male. When the female performs these movements, the male begins to ease out of his shell. As he moves out, the females does likewise, keeping her antennular flagellae near the mouth region of the male. The body of the female is completely covered by that of the male in the copulatory position. The cephalothorax of the female does not come completely out of her shell but just far enough to expose the genital openings on the coxopodite of her third pereiopods. The male comes further out of his shell, exposing almost the full length of his cephalothorax. By stretching, the male is able to bring the genital openings on the coxopodite of his fifth pereiopods near the female orifices. The distal segments of the male's fifth pereiopods move rapidly back and forth between the genital orifices during copulation and may aid in the transfer or placement of the spermatophore filaments. The actual copulation lasts between one and five seconds. It is terminated as both animals pull back into their shells rapidly; the female pulls completely down into her shell and the male back to the opposed position, holding the female. It is not known which partner first terminates copulation.

After copulation the male may push the female away and mating is completed. However, that is rare, and a period of postcopulatory behavior usually follows. This is a series of violent and gentle rocking and cheliped movements by the male which appear indistinguishable from precopulatory behavior patterns. There may be some differences between pre- and postcopulatory movements, but none were detected in the matings that I could follow to completion. Postcopulatory behavior may be carried out by the male for up to an hour. Just prior to termination, the female comes up and again moves her chelipeds and antennules in the mouth-eyestalk region of the male. The male then backs away and the pair separates. The male usually leaves the female on her back and may exhibit some aggression towards her as she attempts to right herself.

If a female *Clibanarius tricolor* is examined just after copulation, one finds her exoskeleton is very soft and her abdomen externally void of eggs. However, new eggs are visible in her abdomen. If a male carried out only a short period of postcopulatory behavior this will also be the condition of the female when the pair separates. When a pair is uninterrupted and carries out a complete sequence of postcopulatory behaviors for some minutes, at the termination of this sequence, the female possesses a noticeably harder exoskeleton and most or all of the new eggs are in place on the pleopods. Whether the postcopulatory behavior of the male actually aids the female or simply affords her protection while she is getting the new eggs in place and her exoskeleton is hardening, is not known. If the force of gravity is used in getting the eggs into position (as suggested by the observations of egg placement in *Pagurus prideauxi* by MATTHEWS (1959), the upside-down position in which the female is kept could be an aid to egg placement. As will be shown later, recently moulted individuals are more subject to attack by shell-seeking conspecific individuals and are more apt to lose their shell in a fight, thus postcopulatory behavior by the male may protect the female from attack by other hermit crabs.

A few multiple copulations by females have been observed but appeared to be rare. Males have been observed to mate with three and four different females in one day.

In a number of pilot experiments, mating pairs of *Clibanarius tricolor* were separated and the male and female placed in a small dish. In very few cases did the male show any orienting preference toward the "ripe" female over the control male or female in the dish. When a male did come into physical contact with a ripe female he usually grasped her immediately. But often a male would pass within a centimeter of a female and show no change in behavior. When a male did orient directly over some distance, it was immediately upon placement in the observation dish and presumably was visually directed. Experiments using ripe females and control animals contained in small pieces of cloth and offered to males also failed to support the idea of any distant chemical orientation by the male. In one case, a male did pick up the cloth containing a ripe female after "wandering" into contact, and held it in his ambulatories for several minutes before moving on. Considering the dense aggregation of individuals in which a ripe female would be located, the absence of distance chemical orientation may not be unreasonable.

From casual observations, the presence of a lunar cycle in the mating activity of some species was suggested. It was reasoned that since ovulation and mating are closely associated, the presence of new eggs and thus the size of the eggs carried by females would show the presence of such a cycle. Collections of 20–25 crabs were made every three days during the month of July, 1963. Later, the egg diameters of the females of these collections were measured, using an A/O Spencer dissecting microscope with eyepiece scale. The results are shown in Figure 12. On July 1 and 10, only 50% of the females were carrying eggs externally. The percentage was higher on most other collection days. Although the limited data gathered does not negate the existence of a lunar cycle and possible supports the idea (the gradual increase in egg size after a full moon peak and decrease), it is not definite evidence for such a phenomenon.

Clibanarius tricolor is a very useful animal for observational work on social behavior. It is common in Curaçao and most of the Caribbean area and its ecological limitation to shallow water makes field work practicable. Moreover, it shows all the aspects of social interaction observed in hermit crabs. Aggressive interactions occur continuously in a large group. In an aggregation, such as described above, observations of shell-fighting and sexual behavior are readily

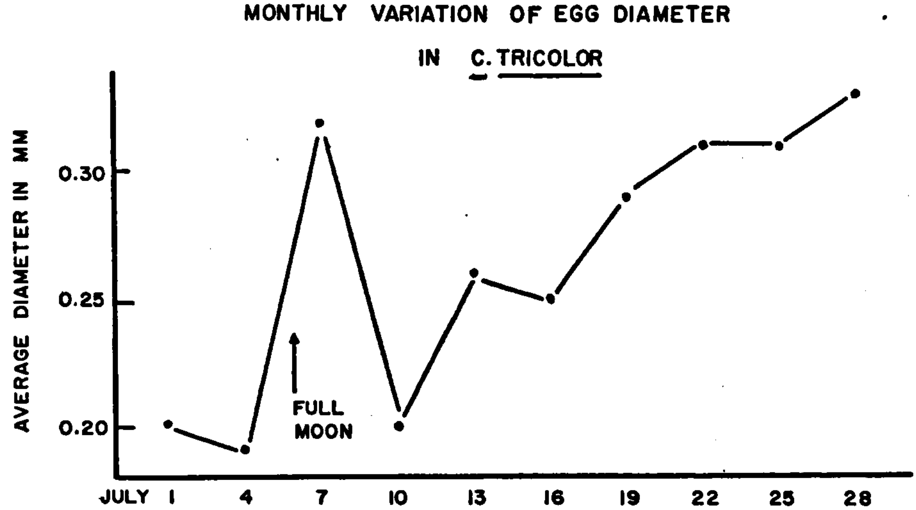


Fig. 12. Variation in average egg diameter in *Clibanarius tricolor* during May, 1963.

carried out. In a group of about 3,000 crabs, it is usually possible to see at least one pair of crabs in sexual activities in less than 15 minutes of observation. Shell-fighting appeared less frequently, but 15 to 30 minutes of careful observation usually allowed detection of one or more shell-fights. Sexual behavior was seen 36 times and shell-fighting interactions 11 times during the observation of 2,000 interactions in this species.

Sexual behavior and shell-fights occurred both night and day although, as might be expected from the marked diurnal grouping, interactions tended to occur more in the day. In order to measure the diel variation of activity in certain aspects of the behavior of *Clibanarius tricolor,* populations of 20 individuals were established in small glass aquaria in the laboratory. The aquaria were marked on the outside with lines at three cm intervals. No food was placed in the tanks for the duration of the observations. The animals were observed during half-hour periods throughout the 24 hours. Two sets of crabs were observed (March 11 and April 4). The number of times any crab crossed one of the lines was recorded and the total crossings of the members of the group was used as a measure of the level of general locomotor activity. The number of crabs moving their chelipeds up and down, as if feeding, were recorded during each minute of observation. The total number of crab-minutes was used as an indication of the level of feeding activity in each half-hour period. As a measure of the level of aggressive behavior, the number of aggressive displays executed by members of the group under observation, was counted during each period. Observations at night were carried out with a "red light" for illumination. (Observations in the field and laboratory indicated that white light sources, when covered with heavy red cellophane were sufficiently "red" to allow observation of the organisms without disturbing their behavior patterns.) Figure 13 shows the results of the diel observations. As would be predicted from field observations, *Clibanarius tricolor* is relatively quiescent during the day and feeds more intensively at night.

Clibanarius antillensis Stimpson, 1862

(Family Diogenidae)

This crab is very closely related to *Clibanarius tricolor* and is morphologically almost identical. Live specimens are easily distinguished by their color pattern. The ambulatory legs are marked with black and white lengthwise stripes in contrast to *tricolor's* blue, yellow and orange bands and white tips. This species was very rare on Curaçao and few specimens were collected. Because so few were found, the observations reported here are considered preliminary, subject to verification and extension in localities where *antillensis* is more common.

On Curaçao, the majority of the specimens were found inside Piscadera Baai on the inner mudflats. A few were found individually among groups of *Clibanarius tricolor* in front of Carmabi, however most were located in parts of the Piscadera inner bay in which very few specimens of *C. tricolor* were found. These mangrove mudflats yielded the few small groups of five to ten individuals found. Observations

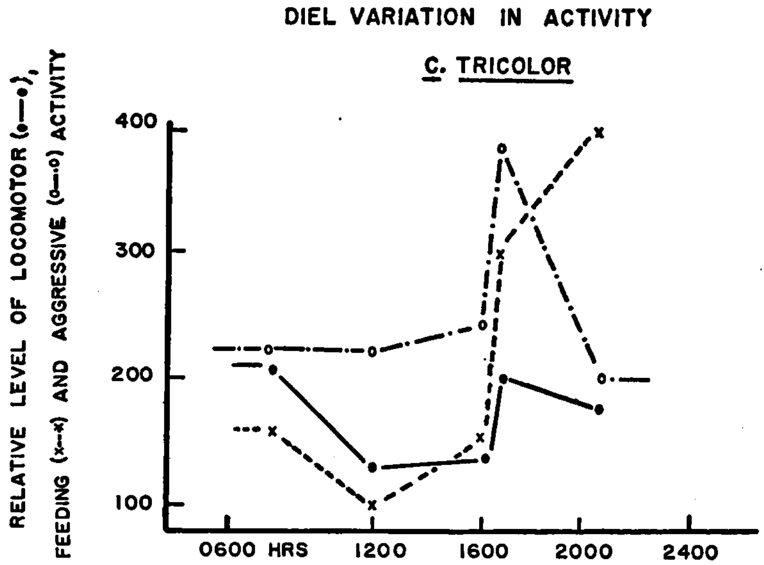


Fig. 13. Diel variation in activities of *Clibanarius tricolor*; average of two days measurement. Relative levels of locomotor and feeding activity show nocturnal pattern; aggressive activity shows evening peak.

around Biscayne Bay, Miami, Florida, indicated that *antillensis* is not limited to such an environment and, at least in Miami, can be found in the same micro environment as *tricolor*.

Behaviorally, *Clibanarius antillensis* appears to be almost identical with *C. tricolor*. Although further investigation may reveal differences in some quantitative aspects or the proportions of certain behaviors, qualitatively the two species are very similar.

The aggressive behavior repertoire is the same as that of *tricolor*; the only noticeable difference was the more frequent use of the cheliped extension in *antillensis*. While walking or when standing still, individuals tended to move their first ambulatories about in front on themselves more than in *tricolor*. Single ambulatory raises were executed with the limb in any forward-back position.

The shell-fighting behavior is also very similar to that of *Clibanarius tricolor*, although, during rapping movements, the aggressor tended to move from the down to the up position a bit more slowly. This motion averaged over 0.24 seconds in *C. antillensis*.

Copulation was observed only once in *Clibanarius antillensis*. The mating pair was noticed as the male was gently rocking the female. This pattern and the other behaviors observed were indistinguishable from those of *C. tricolor*. The gentle rocking moved the shell of the female through 5–10° arc at a rate of 0.72 seconds per cycle. The violent rocking which occurred later moved the female through 40° at a rate of 0.60 seconds per cycle. Just before the female came partially out of her shell for copulation, she moved her antennules alternately against the eyestalk-antennule region of the male. The copulatory position was the same as in *tricolor* and copulation lasted five seconds. About 20 minutes of postcopulatory behavior by the male occurred before the female was pushed away. No new eggs were present externally on the female 50 minutes after copulation. The female exoskeleton was soft at that time and bits of spermatophore filaments were present on the coxopodites of the third and fourth pereiopods.

On one occasion, a ripe female *tricolor* just separated from a male, was placed near a male *antillensis*. The male moved toward and grasped the female with his ambulatories and moved her into the opposed position. After some investigation with his chelipeds, he began precopulatory behavior. He rocked the female *tricolor* gently and violently for about ten minutes before releasing her and moving away. The female had remained withdrawn into her shell during the entire sequence.

The diel variation in activity was measured in the laboratory in the manner described for *Clibanarius tricolor* except that ten crabs instead of 20 were used. The results are shown in Figure 14. These results resemble those of *tricolor* with the exception that there is a peak in the feeding activity in the afternoon

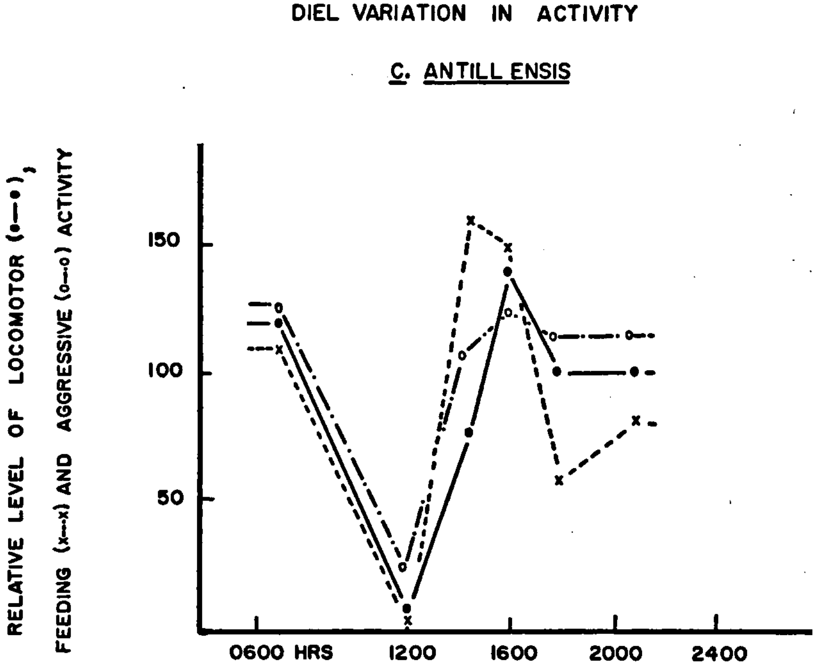


Fig. 14. Diel variation in activities of *Clibanarius antillensis*. Relative levels of locomotor, feeding and aggressive activity show crepuscular pattern. Evening peak earlier than in *C. tricolor*.

accompanying the peak in the locomotor activity. In addition, the afternoon increase in activities began and reached a peak several hours earlier in *antillensis*.

Clibanarius cubensis (Saussure, 1858)

(Family Diogenidae)

This medium to large hermit crab is moderately common on Curaçao. It is much larger than *Clibanarius tricolor*, specimens 10 to 15 mm in cephalothorax length being not at all uncommon. The organism is rather drab in appearance. Olive-green stripes on a brownish background characterize the long ambulatory legs.

Both in the laboratory and in the field, this crab showed both similarities and differences when compared with the above-mentioned species of the genus. The ambulatory legs of *cubensis* appear proportionately longer and they are held away from the body at a greater angle, than those of *tricolor*.

Clibanarius cubensis was found only on the shallow mudflats inside some protected bays. Small but consistent numbers were found along portions of Piscadera inner bay, Spaanse Water (Brakkeput) and Bartool Baai. In Piscadera Baai and at Brakkeput, the crabs could be located only during high tide, either day or night. As the incoming tide covered the mudflats, the crabs moved up onto them from slightly deeper waters, where they had been concealed by the turbidity of the water. No data were gathered concerning population density or behavior of these crabs in the deeper, turbid waters of these bays.

In general, *Clibanarius cubensis* is a rather slowly moving hermit. During walking this slow nature is exaggerated by the length of the ambulatories and a pronounced upward movement preceding the forward motion of the leg which is necessitated by the curvature of the dactyl and the overall angle of the leg relative to the body. The crab's habit of living and moving about on soft mud may have helped to make the upward element of the walking motion necessary.

The aggressive behavior repertoire of *Clibanarius cubensis* is similar to the other members of the Diogenidae. The single ambulatory raise is the aggressive display most frequently given by a member of an interacting pair. The upward motion is not as rapid as in *C. tricolor*, taking up to a full second to execute. In addition the limb is not straight and rigid during movement, but rather the proximal segments attain the raised position before the distal ones. When fully raised, the dactyl is slightly higher than the other segments of the leg, which are parallel to the substratum.

The dactyl is moved through 35–55° depending on the starting position of the limb. Frequently, in severe aggressive interactions, an individual will execute a short series of ambulatory raises without returning the limb to the substratum. The limb is moved up and down through about 30° without a complete downward motion to the neutral position. This "waving" was seen occasionally but less frequently in *tricolor*. In *cubensis*, the ambulatory raise often but not always had a distinct forward element. In some instances, the limb was moved forward 20–30°, as it was raised and back as it was lowered. The overall motion formed an oval. Not infrequently, the other crab was lightly struck in the eye region at the top of the downward motion.

The chelipeds of *Clibanarius cubensis* are used more frequently in aggressive interactions than those of *C. tricolor*. Moreover, two distinct behavior patterns are observable in *cubensis*. (The small size of *tricolor* would make the detection and recognition of two behavior patterns difficult.) The cheliped extension is somewhat similar to that of *tricolor*. One or both chelipeds, slightly opened, are moved upward through about 70° to a position approximately 20° below the horizontal. The motion is rather slow and variable. Tests described in a later section have shown that the chelipeds in the extended position are aggressive stimuli.

The second behavior pattern involving the chelipeds which occurred in aggressive interactions was the cheliped presentation. This appears to be a less intense aggressive signal and often precedes a cheliped extension. It may involve one or both of the crab's equal chelipeds. A small forward motion brings the dactyl of the cheliped to a position perpendicular to the substratum. The whole body of the crab is raised slightly and the proximal segments of the ambulatories moved outward. The proximal segments of the chelipeds are held at a 45° angle to the substratum. The movements involved are slight but they make the individual appear larger and make the chelipeds more prominent. The chelipeds may be held in this position, dactyls perpendicular to the substratum, for some seconds before the animal either executes a cheliped extension or moves its chelipeds back to the normal position.

Shell-fighting behavior follows the pattern for all diogenid crabs. All movements are rather slow. The positioning movements of the aggressive crab approximately describe a V, the vertical portions of the behavior pattern being more prominent than the side-to-side portions. During the rapping movements that follow positioning, the body-shell of the aggressor is slightly lower with respect to the aperture of the defending crab than in *Clibanarius tricolor*. A complete cycle of the movements of a rap took 1.20 seconds (range 0.72 to 2.10 seconds). The downward motion took 0.12 to 0.18 seconds and was more consistent than the movement bringing the shell back up to the fully raised position. The latter was variable, generally becoming slower as a series of raps was carried out. In one series, the execution of the upward motion lasted 0.36, 0.48, 0.48, and 0.60 seconds for successive raps of the series. Series consisted of fewer raps than in *tricolor*. Series of over 10–15 raps were rather rare. In the fully raised position the shell of the aggressor was pulled back futher than in most species. Up to half of the abdomen was exposed in the fully raised position.

Despite many hours of observation, the complete sexual behavior of *Clibanarius cubensis* was not observed. In only two cases, was definite sexual behavior seen. It is very unfortunate that I was unable to record more of the mating activity, since what was observed is distinctly different from that of the two members of the genus described above. In the first instance, two individuals were observed in an opposed position but both were up and out, their ambulatory legs intermingled and moving up and down among the limbs of the other. The female then grasped two ambulatories of the male with her chelipeds and ducked into her shell. After several minutes she came back out, and there followed a period of mutual pulling of the other's ambulatories with chelipeds. Shortly after this I had to cease observation a few minutes to complete an experiment in progress. When I returned, the pair had separated, and the female was sitting on top of the male shell performing solitary "raps" (a motion similar to the rapping motion of the aggressor of a shell-fight, but the crab is not interacting with any other; this behavior was seen occasionally in females of other species following copulation). The pair separated completely after about 30 minutes. Later examinations showed that the female had spermatophores attached several places on her ventral side, around the bases of the walking legs.

In the second case, a large female had been releasing larvae for

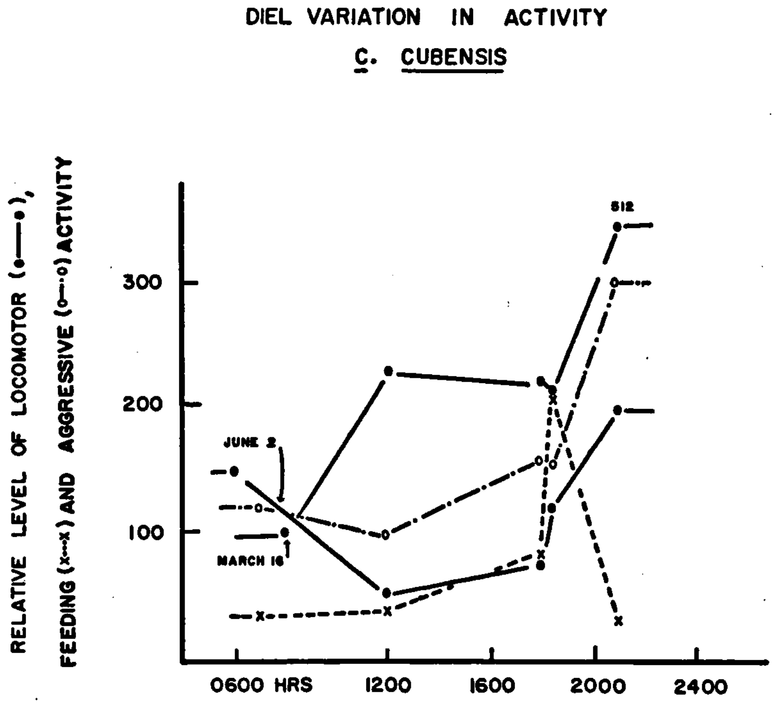


Fig. 15. Diel variation in activities of *Clibanarius cubensis*. Feeding activity shows evening peak; aggressive activity nocturnal; locomotor activity variable, results of both days presented.

some minutes when a male grasped her and moved into the opposed position. The female ducked in and during the subsequent hours of observation very little occurred. However, intermingling of all ambulatories and mutual pulling of ambulatories with chelipeds, while in an opposed position, did occur several times.

The diel variation in activity of *Clibanarius cubensis* is shown in Figure 15. The locomotor activity pattern of variation was rather dissimilar on the two days measured, so each day's results are given rather than an average. It could be that the low level of feeding activity observed during these experiments, was in part due to the sand (rather than mud) bottom in the observation tanks.

Clibanarius vittatus (Bosc, 1802)

(Family Diogenidae)

This species is morphologically and behaviorally very similar to *Clibanarius cubensis*. It is a medium-large, slowly moving crab, averaging only slightly less in size than *C. cubensis*. The species is very rare on Curaçao.

Only two specimens were found, in the shallow grass beds along the west side of the entrance to Spaanse Water. As in the case of *Clibaranius tricolor*, it has not been reported from Curaçao previously. Although one shell-fighting sequence between these two individuals was observed and filmed in Curaçao, the majority of the observations of the behavior patterns of *C. vittatus* wers carried out in Miami, Florida. Specimens were collected on the shallow sand and mudflats along the northeast side of Key Biscayne, in Bear Cut, not far from The Institute of Marine Science of the University of Miami. As with *C. cubensis*, some of the crabs seemed to move shoreward following high tide and retreat to somewhat deeper water as the tide went down. Very few specimens of *cubensis* were found in this area along Bear Cut, where *vittatus* was rather common.

Behaviorally, *Clibanarius vittatus* is almost identical to *C. cubensis*. Their behavioral repertoires appear to be the same and both seem to use the various displays in similar situations and proportions. The position of the chelipeds in the fully extended position was a bit higher, the dactyl having moved through 100°, to a position almost completely parallel to the substratum. The cheliped presentation display was the same as in *cubensis* and was common in aggressive interactions. In both species, the dactyls are lifted off the substratum in the presentation position.

Clibanarius vittatus has two types of ambulatory movements: the standard raise which has little (5–10°) forward movement and a forwardly directed movement which often strikes the shell or head region of the other crab. This forward ambulatory movement was often used by an aggressor as it was moving into an opposed position and it appeared to be successful in "causing" the other crab to duck down into its shell. As in all hermit crabs observed, after an individual has been turned on its back and pulled back into its shell, it comes into view in a characteristic posture. The chelipeds are slightly raised, separated and the dactyls opened slightly. All four ambulatories are fully spread and held in a position similar to a quadruple raise. The first and second ambulatories form a 20° angle with each other in this defensive position. The crab usually holds its first ambulatories in a spread position as it uses the second pair to attain an upright position.

The shell-fighting behavior presented only minor variations from that of *Clibanarius cubensis*. The positioning movements had more side-to-side elements. The motion of the aggressor's body-shell described a horizontal figure 8, over but slightly below the aperature of the defender. The rapping movements were slow, although the attacker did move from the out to in position rapidly (0.06 seconds). The movement outward took 0.66 to 1.14 seconds. The entire cycles ranged in duration from 1.98 to 2.22 seconds. The shell movement involved in a rap varied from about the length of the eyestalks to the full length of the cephalothorax.

Definite sexual behavior was seen once in *Clibanarius vittatus* and another sequence, similar to that seen in *C. cubensis* was observed. In this latter interaction, a male was holding a female in the opposed position while grasping her first ambulatories in his chelipeds. He pulled her about the observation tank while holding onto these ambulatories and at one time gave a short series of rocking motions about an axis through the plane of the female aperture. This followed some cheliped movements up and down in the aperture. However, nothing more happened and the pair separated. No spermatophores were found.

In the one complete sequence of sexual behavior seen, the larger male (23.0 mm c.l.) was observed holding his ambulatories over and around the female (19.0 mm c.l.) who was upright, ambulatories on the substrate. About ten minutes after initial observation, the male turned the female into an opposed position. The female remained partially out, appendage visible for some time. During this time and later when the female ducked down into her shell, the male tapped at the rim of the aperture, chelipeds and ambulatories with his own cheliped. These short tapping movements were executed by both chelipeds, both alternately and simultaneously. The simultaneous movement of both appendages occurred more frequently in the latter minutes of precopulatory activity. It appeared that the female shell and limbs were usually lightly touched by the male's dactyls, although some movements did not touch any part of the female or her shell. After about an hour of male tapping, the female began moving her chelipeds against the male's. Shortly after this, the male and female eased out to the copulatory position, ventral surfaces apposed and ambulatories intermingled. Copulation lasted five seconds. Shortly after copulation the male let the female get into an upright position however, he kept his ambulatories around her for 15 minutes. The female had many eggs in place and many not yet in place when examined.

The diel pattern of activity of *Clibanarius vittatus* was not measured.

Calcinus tibicen (Herbst, 1791)

(Family Diogenidae)

This abundant, widespread crab was the second most common species on Curaçao. It is a medium-small species, individuals averaging 8–10 mm in cephalothorax length. The left cheliped is markedly larger than the right. The chelae and ambulatories of the majority of specimens are dark red-brown with white tips. A second, olive-green color phase was occasionally collected on Curaçao; however, matings were observed between the two types so it is assumed that they represent only color phases of the same species.

Calcinus tibicen was found in shallow, open waters almost everywhere around Curaçao. Although not present in enclosed bays away from open circulation, it was otherwise as widespread as _Clibanarius tricolor_. It was found in the same type of habitat as _tricolor_ although more plastic in its depth restrictions. In some areas, the crabs are in water less than ten cm in depth. In other localities they are common on rocks and coral fronds three meters deep.

The diel variations in behavior observed in the field were not as marked as in *Clibanarius tricolor*. Likewise, this species did aggregate, but not as consistently as *tricolor*. When grouping occurred, the groups maintained during the day were small. In slightly deeper water, population often appeared to be distributed at random. However, in shallow water, groups of 15–35 individuals were common. Individuals of *Calcinus tibicen* were relatively quiet during the day. Just a few individuals could be seen moving about a little and picking at the detritus-covered rocks during the morning and early afternoon. Around 16.30–17.00 hrs, movement and feeding activities started to increase. Between 17.00–18.00 hrs, most of the individuals moved out of the restricted areas occupied during the day. This movement often appeared to be in several, if not all directions for the members of any one group. Between 05.30 and 06.00 hrs (the sky was light but the sun was not yet up), the crabs moved back into the area of diurnal aggregation and became quiet – often withdrawing into their shells.

One group of about 35 individuals, located directly in front of the Carmabi, in about 30 cm of water were especially interesting in their diel movements. These crabs shared the interior of a submerged iron pipe with a medium size moray eel. The pipe was ten cm in diameter and resting on a rock at one end, such that the middle of the pipe, where the majority of the crabs grouped, was ten cm above the sand bottom. A large hole in the middle of the pipe permitted observation of most of the crabs. Some of these were removed (until the moray eel interrupted), marked with waterproof ink and replaced for further observations. Following initial losses, the number of marked individuals in the pipe during the day remained constant from August 18 to 26, when observations were discontinued. It was found that the crabs moved out in the evening by (1) crawling down the interior of the pipe to the bottom, (2) crawling on the pipe exterior to the bottom, or (3) up the pipe exterior to the rock the pipe was resting on and starting feeding activity there. However, in the early morning, all the crabs observed followed

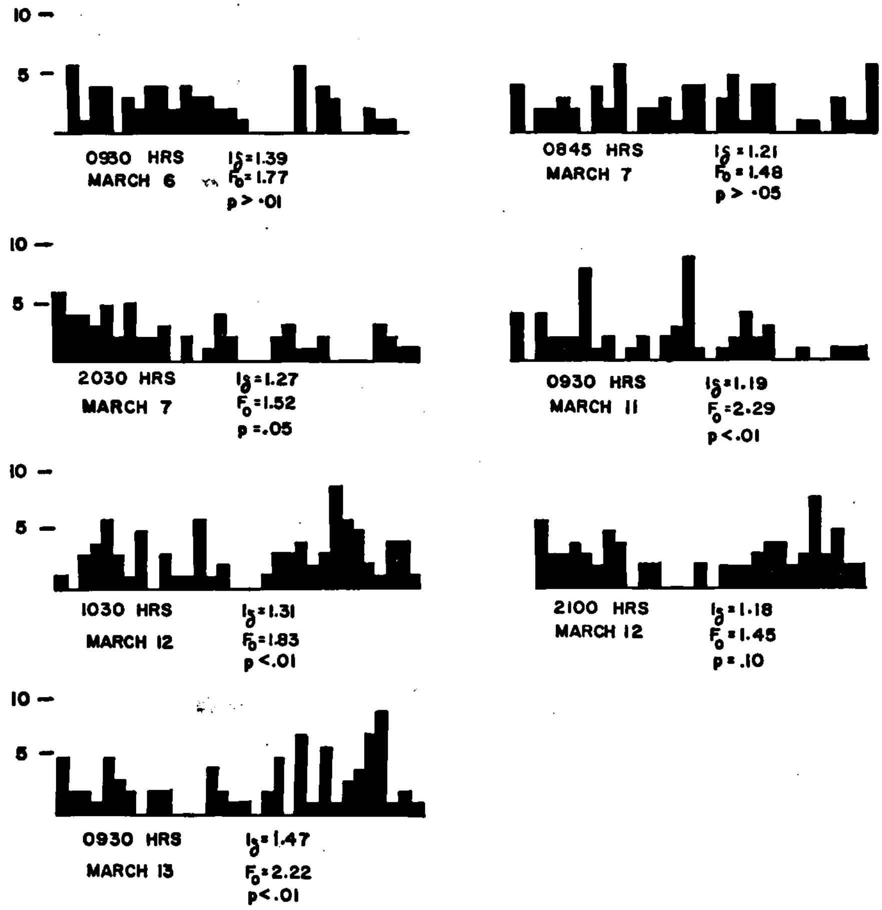


Fig. 16. Laboratory distributions of *Calcinus tibicen*. Histograms of number of individuals found in 32 equal segments of circular container.

TABLE 4

FIELD DISTRIBUTIONS OF *Calcinus tibicen*

Carmabi

n	f	nf
0	59	0
1	3	3
17	1	17
20	1	20

$q = 64$ $N = 40$

$I_\delta = 26.69$
$F_0 = 16.90$
$p < .01$

Boca St. Michiel

n	f	nf
0	10	0
3	1	3
8	1	8
21	1	21
31	1	31
191	1	191

$q = 15$ $N = 254$

$I_\delta = 8.79$
$F_0 = 141.78$
$p < .01$

Spaanse Water

n	f	nf
0	12	0
1	2	2
2	3	6
3	3	9
5	1	5
6	1	6
7	1	7
13	1	13

$q = 24$ $N = 48$

$I_\delta = 2.88$
$F_0 = 4.83$
$p < .01$

Piscadera Baai Channel

n	f	nf
0	18	0
1	3	3
2	2	4
3	1	3
4	2	8
5	1	5
6	1	6
7	1	7
11	1	11
12	2	24

$q = 32$ $N = 59$

$I_\delta = 3.43$
$F_0 = 5.52$
$p < .01$

route (1) back to the grouping area, crawling up the interior of the pipe after entering at the lower end. In this population there was very little movement or feeding during the day although two matings between a large red-brown male and two different olive-green females were seen.

Field distribution measurements were taken as for *Clibanarius tricolor.* The results and the accompanying statistics are given in Table 4. It can be seen that the distributions measured are rather strongly contagious. The distribution of individuals in a uniform circular container in the laboratory was measured as in *tricolor*; the results are shown in Figure 16 for the two populations established. Accepting $p = .01$ as the level of significance for the non-randomness of such distributions, it is evident that two of the diurnal and both of the nocturnal lab distributions measured were random. Even those counts which are statistically contagious are so only to a slight degree. *Calcinus tibicen* tends to group on or under large rocks during the day and the non-randomness of the crab's distribution may be due to orientation toward some non-random physical factor of their environment rather than the presence of conspecific individuals.

Calcinus tibicen is an active crab but its movements are slower than those of *Clibanarius tricolor.* Individuals of *tibicen* execute the ambulatory movements described for *tricolor* and the patterns of movement are very similar. The full movement of the ambulatory is through about 60°, bringing the limb to 10° below the horizontal.

Both of the chelipeds are employed in aggressive interactions. All possible variations (major cheliped, minor or both) of the two types of cheliped movements do occur. The movements of the major cheliped are more common than those of the minor. *Calcinus tibicen* does execute a presentation as well as an extension movement. An extension is often carried out from the presentation position. The movement and posture of the limbs, when executing a cheliped presentation, are similar to those described for *Clibanarius cubensis.* The body is raised slightly as the cheliped(s) is moved forward until the dactyl is perpendicular to the substrate. This posture is often maintained for a number of seconds.

The cheliped extension is a slow but strong movement. In intense interactions, two individuals may mutually block the full movement of the chelipeds by repeated and sustained contact between chelipeds. This pushing is physically forceful as evidenced by the speed and distance one individual may be thrown if it loses its footing. However, interactions of this type are not nearly as frequent as in pagurid species. The dactyl of the cheliped is moved through 85–90° to a position slightly below the horizontal. The movement from a neutral to a fully extended position takes 0.54–0.72 seconds; an extension from the presentation attitude may take only 0.48 seconds.

The shell-fighting behavior of *Calcinus tibicen* is very similar to that of *Clibanarius tricolor* with respect to spatial relationships, positioning movements and general execution of rapping. The initial positioning movements prior to rapping were not always extensive. However, positioning and rotating movements by the aggressor were more common before and between subsequent series of raps. The aggressor moves approximately in a wide figure 8 over the aperture of the defending crab. The vertical portion of the movement is equal to 20–25° arc. The downward rapping motion was always completed in one frame of film, i.e. lasted 0.06 seconds or less. The complete rapping cycles lasted 0.30 to 0.72 seconds, and unlike *Clibanarius cubensis* and *vittatus* the shell was held in the fully raised position longer than in the fully lowered position.

In an effort to elucidate several aspects of hermit crab social behavior, an attempt was made to provide some individuals with clear plastic shells of an appropriate size. The interior of the shells was an exact replica of the interior of natural shells while a smooth hyperbolic cone was used for the external shape. (These shells were made by Mr. R. J. HAZLETT and the author.) The only common species, which was large enough for the smallest shells available in quantity was *Calcinus tibicen*. It was hoped that with these transparent shells, the relationship of the chelipeds of the two crabs could be observed, when an attacking crab goes into the defender's shell and carries out rapping motions. Fully realizing the limitations of single observations, this problem has at least a tentative answer. On one occasion, two *Calcinus tibicen*, both in plastic shells, were observed engaged in a shell fight. In this interaction, the aggressor fought for and won a shell of the same interior size and shape but smaller external size and overall weight. After positioning movements and some rapping with all ambulatories around the other's aperture, the large attacking crab went inside the shell aperture of the defending crab. While the attacking crab was outside, with major cheliped resting just inside the aperture, the defending crab's position had varied from one of complete withdrawal into its shell to a position rather far forward, with the major cheliped in contact with, but not interlocked or grasped by, that of the aggressor. As the aggressor moved head-first into the other shell, the other crab retreated as far as possible to the inner whorls of the shell. Eventually the cephalothorax of the aggressor was completely in the other shell. At the farthest intrusion of the attacker, the major chelipeds of the pair were not touching. The attacker then began rapping and as the motion gradually increased in intensity, the defending crab moved forward, occasionally making slight major cheliped contact with the attacker. The attacker backed out, continually rapping, until he had backed out completely and the defending crab came completely out of its shell. At no time during this interaction were the chelipeds interlocked or used to pull at any portion of the defending crab.

The sexual behavior of *Calcinus tibicen* resembles that of *Clibanarius tricolor* in general form. The male holds the female, which is always smaller (averaged 41% smaller in c.l., range 29–57%), in the opposed position. Although some cheliped movements in the female aperture do occur, the precopulatory activity consists largely of rotating movements. There is not a clear differentiation into two types or intensities of rotating-shaking as in *tricolor*. The male moves the female 60–75°, around an axis perpendicular to and through the plane of the female aperture. Although tending somewhat toward the asynchronous figure 8 rotating of *Clibanarius tricolor*, the movement in *Calcinus tibicen* is more nearly circular.

The speed of rotating is 0.36 to 0.72 seconds per cycle (average 0.48 seconds).

Male *Calcinus tibicen* often grasp a female and begin rotating movements when she still has developing larvae on her pleopods. In one case, copulation took place and spermatophores were placed around the genital openings, while the female still had larvae attached. These were large larvae (0.50–0.60 mm long) and possibly would have been released within a few hours. I have not observed the female moult during precopulatory activity and do not know if the male assists the female in moulting.

On two occasions, it was possible to interrupt the precopulatory activity of a pair, place the female *Calcinus tibicen* in a clear plastic shell and observe the subsequent mating activity. In one case, the female still had a full batch of developing eggs, and the male only intermittently held the female (in the clear shell) for the first eight hours following her placement in the shell. During this time the female released a number of larvae, but still had many on her pleopods when the pair was separated for the night. By morning, the female had released all her larvae but there was no shed exoskeleton visible, so it is possible that she did not moult. However, she may have moulted and the new exoskeleton hardened. When the pair was placed together, mating took place rapidly and copulation lasted about eight seconds. During copulation, the distal segments of the fifth pereiopods of the male could be seen moving back and forth between the closely placed male and female genital openings. Later examination of the female revealed spermatophore material around the bases of the third, fourth and fifth pereiopods and on the upper abdomen.

With the aid of plastic shells, it was observed that, at least in the period just prior to copulation, a regular sequence of male-female interactions takes place: the male rocks the female, she moves up within her shell and touches the males' major cheliped (resting in her shell aperture) with her own, he taps the female with his major or minor cheliped and she finally ducks back into her shell. After a number of these cycles, the last portions of the cycle are omitted, the female comes up further, tapping the male in the mouth-eyestalk region with her antennules and/or minor cheliped. The male and then the female ease out to the copulatory position and copulation takes place.

In most cases where the female was examined within several hours after copulation, she was soft, indicating a recent moult. The placement of new eggs on the pleopods does not follow copulation as closely as in *Clibanarius tricolor.* Of the six matings in which copulation was observed, only one was followed long enough after copulation to see some new eggs in place; in one of the female-in-plastic-shell matings, a few new (0.30 mm long), bright orange eggs were in place ten hours after copulation. There is little or no post-copulatory behavior by the male; the female is pushed or thrown away almost immediately following copulation.

As with *Clibanarius tricolor,* collections were made systematically throughout one month and the egg diameters measured. The

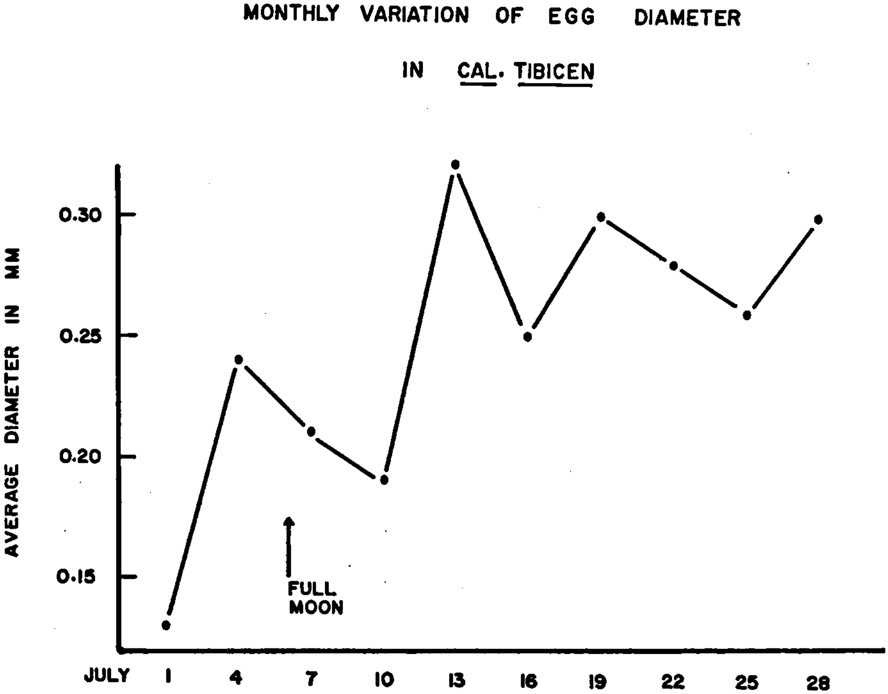


Fig. 17. Variation in average egg diameter in *Calcinus tibicen* during May, 1963.

results are shown in Figure 17. Again the data neither negates nor really strongly supports the idea of a lunar cycle in mating activity. The average size of the females' eggs did decrease and then rise to a higher level as one might expect if the crabs mated (releasing the large old eggs, attaching the small new eggs) more frequently about the time of the full moon – July 6. However, the pattern is not smooth or consistent.

The diel variation in activity was measured as in other species and the results are shown in Figure 18. The decrease in feeding activity at night is not consistent with field observations, but otherwise the locomotor and feeding activity variation patterns appear to represent the same sort of patterns as were observed in the field.

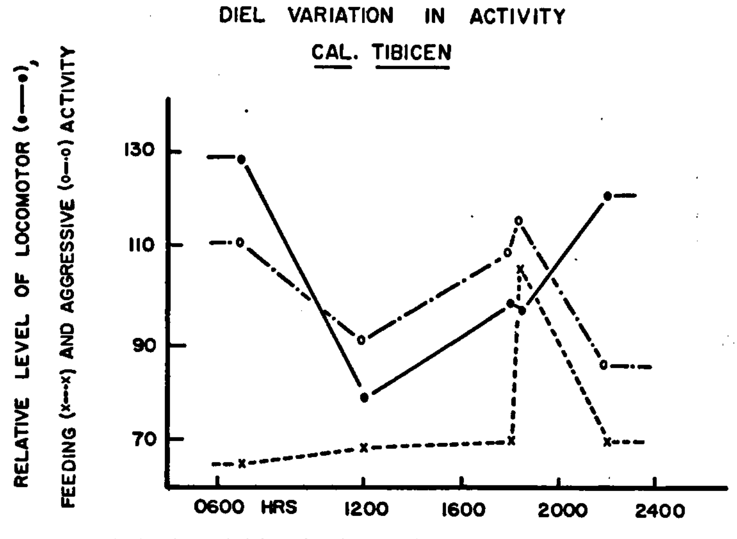


Fig. 18. Diel variation in activities of *Calcinus tibicen*. Feeding activity shows evening peak; aggressive activity crepuscular; locomotor activity nocturnal.

Paguristes cadenati Forest, 1954

(Family Diogenidae)

This member of the deep-water genus *Paguristes* has not been reported from Curaçao previously. It is a medium size species, averaging about 8–10 mm in cephalothorax length. The color of the ambulatories and equal chelipeds is a very striking bright red.

Paguristes cadenati was collected mainly with scuba equipment, at several locations along the south shore of Curaçao. A few specimens were collected in the entrance to Spaanse Water. More specimens were found on reef formations between Willemstad and Piscadera Baai only below five meters and although most abundant at about 10 meters, crabs were found down to about 15 meters. Between 15 and 25 meters, no specimens were found in the areas observed.

Neither collecting nor field observations were carried out at night.

The aggressive behavior repertoire of *Paguristes cadenati* is similar to those of other diogenid crabs and in particular that of *Clibanarius cubensis*. It is rather slow in its general speed of movements. As in *C. cubensis*, the vertical element of normal walking movements appear more prominent than in species such as *Clibanarius tricolor*. Both the ambulatories and the sculptured chelipeds are used in aggressive interactions. There are two types of stereotyped ambulatory movements; the standard ambulatory raise which involves little forward movement, and a forward ambulatory movement. In the standard raise, the appendage is moved vertically through about 60° until the limb is almost horizontal. The leg is held rather rigidly during movement although the dactyl often does not complete its motion until the other segments are in place. The upward motion is carried out in 0.12 to 0.24 seconds. The second type of ambulatory movement is more complicated. The dactyl of the limb is moved in an imperfect circle, which is a bit flattened and pointed anteriorly. The limb is initially moved posteriorly and up and reaches a high point, horizontal to the substratum or a little higher, as it is brought forward over the neutral limb position. From there the leg is moved forward and down, in a straight line to the point of furthest forward movement, about 45° forward from the neutral position. From here it is brought down and back. The entire motion is relatively uninterrupted and smooth.

The upward motion takes about 0.36 seconds while the forward-down-back motion takes 0.72 seconds. This latter movement was not as common as the standard ambulatory raise.

Paguristes cadenati also has two types of aggressive cheliped movements – the cheliped presentation and cheliped extension. The presentation is as in *Clibanarius cubensis*; the cheliped extension brings the appendage to a position just below the horizontal in about 0.24 seconds.

Shell-fighting behavior, positioning and rapping proceed as in other crabs. The downward motion of the rapping pattern always occurred in less than 0.06 seconds. The upward motion was rather quick, taking 0.18 to 0.24 seconds. The majority of time of each cycle was spent with the aggressor in the fully down position. In this respect, *Paguristes cadenati* resembles *Clibanarius cubensis* and *C. vittatus*. Rapping cycles vary in duration from 1.20 to 1.26 seconds. During rapping, the shell of the aggressor moved a distance equal to as much as one half the length of the cephalothorax. Series of raps in this species generally did not include as many raps as in most species. In one interaction, the loser was extracted after only nine raps. In addition, the aggressor clearly "helped" the loser out of its shell by pulling on its chelipeds with its own chelipeds.

The sexual behavior of *Paguristes cadenati* can occur before the female has moulted, while she is still carrying a set of well-developed eggs. In three of the four matings observed, the pair copulated and separated while the female was carrying a well-developed brood. The sexual behavior involves a number of patterns of movements. From an opposed position, with his chelipeds just in the aperture of the female, the male moves her shell back and forth about an axis running parallel to the female columella axis, at right angles to the anterior-posterior axis of the male; and he may execute another movement, about an axis through and perpendicular to the plane of the female aperture. In addition to these two types or rotating movements, the male moves the female from side to side along the length of the first-mentioned axis. In all these movements, occasionally the male rather than the female moves during these behavior patterns. This is more common when the female is almost as large as the male. The males of *Paguristes cadenati* in the observed matings were 3–85% larger (average 41%) than the females.

In addition to rotating and shaking movements, the male often carried out a short series of cheliped movements during precopulatory behavior. The chelipeds are moved up and down alternately in the aperture of the female. After some minutes of all these behavior patterns, the female began to move out of her shell. As the female moved up, the male grasped either her ambulatories or chelipeds with his chelipeds and appeared to pull the female out. If her chelipeds were free, the female moved antennules and chelipeds about in the eyestalk-mouth region of the male. Both crabs then moved out of their shells – further than in the other species studied. The anterior of the male's abdomen was clearly exposed when in copula. In the copulatory position, the ambulatories of both sexes are fully extended and intermingled (similar to the position seen in the precopulatory sequences of *Clibanarius cubensis*);

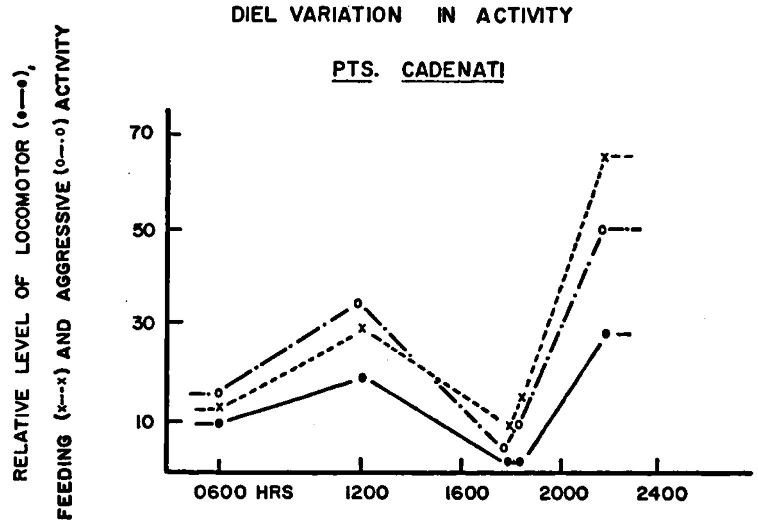


Fig. 19. Diel variation in activities of *Paguristes cadenati*. All activities anti-crepuscular, nocturnal.

the male chelipeds continue to hold onto female appendages and are doubled back. The fifth pereiopods of the male move between the pair during copulation and the posterior part of the male cephalothorax moves up and down periodically during copulation. Unlike other hermit crabs, the pairs remained in copula for many seconds and in one case for two minutes. No long-term postcopulatory behavior was observed. The male did move its chelipeds up and down and rotate the female for about a minute in several cases, but the female appeared to succeed in chasing the male away and attaining the upright position rather quickly after copulation. In the one case where the postcopulatory female had new eggs in place when examined, she had not been disturbed or her shell opened until 42 hours after copulation.

The diel variation in activity is shown in Figure 19. As can be seen, the crab is active in an anti-crepuscular pattern with a nocturnal emphasis. This applies to both the locomotor and feeding behavior. Perhaps the decrease in activity at dawn and dusk may enable *Pts. cadenati* to avoid competition with and/or predation by crepuscular organisms.

Paguristes grayi Benedict, 1901

(Family Diogenidae)

This medium to large crab was found in several locations around Curaçao. It was not abundant in any locality. It was not found on large reef formations but did occur on or near fronds of elkhorn coral.

The most consistent sources of *Paguristes grayi* were the entrance to Piscadera Baai and the west side of the entrance of Spaanse Water. Smaller individuals were frequently found outside octopus lairs. This could be for feeding purposes or the obtaining of octopus-emptied shells or both. The specimens collected in the entrance to Piscadera Baai averaged about 20 mm in c.l. The crabs collected in 2–6 meters of water at Spaans Water were larger, averaging about 30 mm in c.l., with some individuals being up to 60 mm c.l. The most consistent features of its environment seemed to be a sandy-rocky bottom in open water and elkhorn coral formations. It was often found high on the fronds of colonies of this organism.

Of the crabs studied, *Paguristes grayi* was definitely the slowest moving. Not only did it walk and climb about slowly, but its aggressive displays were also carried out very slowly. In its walking movements it resembles *Clibanarius tricolor* more than *Paguristes cadenati*. It does not move very much at any time and a group in an aquarium may show no active social behavior for many minutes or even hours. During the day or at night, a good percentage of the animals in any population (in the laboratory or field) are pulled back into their shells. Social interactions do occur but at a low rate. I have not knowingly seen any phase of the sexual behavior of *grayi* and only on a few occasions have I seen definite shell-fighting behavior.

The crabs do show aggressive behavior and interactions take place in a manner similar to that of other species; these interactions often appear as if the animals were being viewed in slow motion.

The ambulatory raise in *Paguristes grayi* is a movement which brings the limb rigidly to a position about 10° below the horizontal. Both single and double raises were executed by interacting crabs. As with the other aggressive behavior patterns, "incomplete" behaviors and variability in the execution of these aggressive displays appeared more frequently in *grayi* than the other species studied. Sometimes the motion up and down of an ambulatory was complicated by an oval motion at the top – the limb being brought down and slightly forward, then raised back and up after moving to a position about halfway down. Perhaps this was just a second "raise" without bringing the limb down completely.

A set of movements similar to the cheliped presentation of *Clibanarius cubensis* was seen on a few occasions. A cheliped extension was seen much more frequently and definitely. Although variable in speed and extent of movement, interacting animals often did raise one or both chelipeds through an arc of about 85° to a position about 10° below the horizontal. Often the dactyl of the cheliped was partially open as it was extended.

Thes hellfighting behavior of *Paguristes grayi* appears to fit the pattern for diogenid crabs. After turning the other crab on its back and attaining an opposed position, the attacker goes through positioning behavior in which its body moves back and forth over the defender's aperture in a horizontal figure 8. Rapping behavior may follow; the rate of rapping was estimated at 1.5 seconds per cycle or longer. The attacker's shell is moved about half the length of the cephalothorax in raps of the greatest movement. Whereas shell-fights in other species last a number of minutes, the interactions of *grayi* last for hours or even days. Extended periods of inactivity occur between series of raps. One pair was observed frequently for over 48 hours, during which time the attacker carried out three series of rapping motions. As in *Paguristes cadenati*, in the few successful fights observed to completion, the winning crab was holding the chelipeds of the loser with his own and appeared to be pulling the loser out. Occasionally the attacker rotated the defending crab back and forth around an axis perpendicular to and through the aperture of the defending crab.

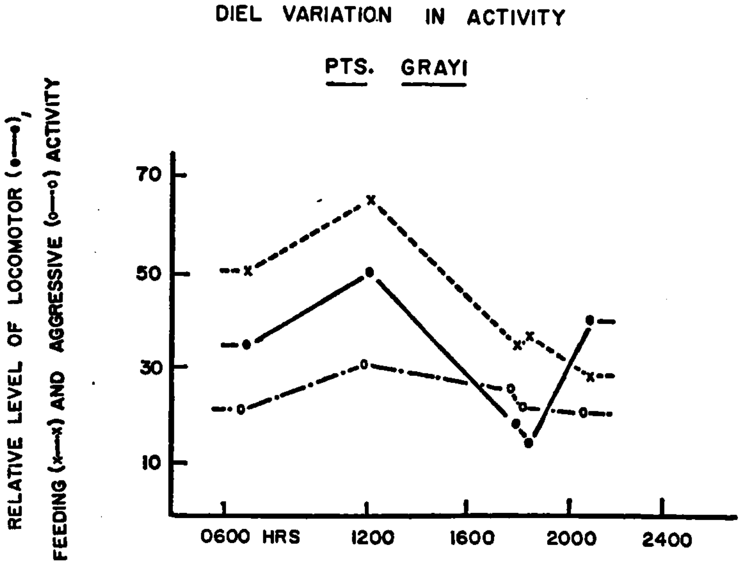


Fig. 20. Diel variation in activities of *Paguristes grayi*. Feeding diurnal; locomotor activity anti-crepuscular.

The diel variation in activity, as measured in the laboratory, is shown in Figure 20. As in *Paguristes cadenati*, the locomotor activity shows an anti-crepuscular pattern. Feeding appears to be confined more completely to the diurnal hours.

Pagurus miamensis Provenzano, 1959

(Family Paguridae)

The behavioral differences between diogenid and pagurid crabs proved to be rather extensive and consistent. Although the two families possess the same classes of behavior, a number of differences between them became apparent during this study. These differences will be described in more detail under *Pagurus miamensis*. The other species of *Pagurus* and *Pylopagurus* studied showed only minor variations on the family theme.

Pagurus miamensis is a small, active species which is widespread around Curaçao (although previously unreported from the island). It is a black and white crab averaging about 3 mm in c.l. As is characteristic of the genus, *miamensis* has unequal chelipeds, the right being distinctly larger. This species is being considered first among the pagurid species because of the relatively greater amount of work done with it.

Pagurus miamensis was present in many shallow water locations around Curaçao. Although not as narrowly restricted as *Clibanarius tricolor*, it was only occasionally found below two meters and was most abundant in about one meter of water. It is limited to waters with good circulation and a rocky or reef-covered bottom. Crabs were often found near various types of sessile coelenterates. No specimens were found in the north coast bocas, where the wave action is considerable. It was common in the open waters outside Piscadera Baai, St. Kruis Baai, Boca St. Michiel, Vaersen Baai, Sta. Martha Baai, parts of Spaanse Water and Fuik Baai.

Pagurus miamensis is a nocturnal species, with a diel pattern of movements somewhat similar to that of *Clibanarius tricolor*. In most places, aggregations are present during the day. These aggregations are smaller and never as dense as those of *tricolor*. They may contain up to 100 individuals in an area of about 120 square cm; but even in the most dense groups crabs are not piled up on top of one another. As will be shown later, these crabs appear to orient to the particular rocks they gather on rather than the presence of conspecific individuals (as in *tricolor*). During most of the day, individuals are relatively inactive and withdrawn into their shells. They do not move about or feed to any degree. Around 15.00 hrs the crabs begin to move about and away from the area of aggregation. Concomitant with the increase in locomotor activity, the crabs begin feeding activity, picking at detritus matter with both chelipeds. During the evening and night, the crabs move up to several meters away from their aggregation area. At some time in the early morning they begin to move back toward their aggregation area. By 04.30 hrs many are in the diurnal area and by 05.00 hrs the aggregation is formed and the crabs are beginning to become inactive. Thus *Pagurus miamensis* moves out to feed about one and a half hours before *Clibanarius tricolor* moves out and returns to its aggregation area 3/4 to one hour before that species aggregates.

Two aggregations of *Pagurus miamensis* were marked and daily counts made for several days. The two groups were about one and a half meters apart, partially beneath a submerged iron girder in about 40 cm of water. The larger group contained 186 individuals, was located six meters from shore and was marked with blue ink. The other group contained 60 crabs, was four and a half meters from shore and was marked with black ink. Both were marked and replaced in their respective areas on March 18. The number of marked crabs counted on later days is shown in the table below. It is felt that the large initial decrease in numbers is due more to loss of markings than movement of crabs.

	Black in Black Area	Black Outside	Black in Blue & Blue in Black	Blue Outside	Blue in Blue Area
March 19	12	2	–	4	59
March 20	17	6	1	12	53
March 21	11	3	–	3	50
March 25	12	2	1	–	29
March 26	5	5	–	–	21

In a second marking experiment, a group of crabs that diurnally aggregated on a medium size rock in about 60 cm of water was chosen. Of the 177 *Pagurus miamensis* in the group, 75 were marked and placed back on the rock on July 2. The table below shows the number of marked crabs found on the rock and in the nearby area (three meters in all directions) on subsequent days.

	Number Marked on Rock	Number Marked Outside
July 3	45	0
July 4	35	2
July 5	38	0
July 6	37	0
July 7	29	0
July 8	21	2
July 9	31	0

These observations indicate the presence of rather stable group composition and location in *Pagurus miamensis*.

In a third pilot experiment concerned with the characteristics of aggregations in the field, two rocks were observed for several days. These rocks were inhabited diurnally by five and ten individuals ot *Pagurus miamensis* respectively. The number and position of crabs on these rocks had been constant for three days prior to alternation. The rocks were then moved ten cm closer to shore, after the crabs had left for the evening. The next two days the rocks were inhabited by the same number of crabs on the same parts of these rocks. As indicated by the above tests and by laboratory experiments described in a later section, it appears that *miamensis* orients to physical factors of its diurnal aggregation are rather than the presence of conspecific individuals. The results of field and laboratory distribution measurements are presented in Table 5. As can be seen, *miamensis*'s field distributions are strongly contagious.

The laboratory measurements were all made in small glass aquaria. As with *Clibanarius tricolor*, dense aggregations were not formed under the more uniform conditions peresented in the laboratory; however, the diurnal distributions were contagious. As would be expected, the distribution was random at night.

As shown above, *Pagurus miamensis* is an active species that tends to aggregate. Many social contacts are made without the execution of any aggressive displays. Before the aggressive signals are described, a behavior should be discussed which was not clearly observed in the diogenid crabs studied, but was often seen in *miamensis* and all pagurid crabs observed.

I have called these movements DISLODGING-SHAKING. They are executed by one crab when another crawls onto the back of its shell. The crab being crawled upon rises slightly on its ambulatories, and with its walking legs stationary, moves its body-shell back and forth quickly around an axis perpendicular to and through the plane of its own shell aperture. This short swinging motion (about 30° movement) sometimes physically throws the other crab off; other times the rate of movement of the "offending" crab increases

TABLE 5

FIELD DISTRIBUTIONS OF *Pagurus miamensis*

Carmabi

n	f	nf
0	8	0
1	3	3
2	2	4
4	2	8
177	1	177

$q = 16$ $N = 192$
$I_\delta = 13.60$
$F_0 = 161.40$
$p < .01$

Boca St. Michiel

n	f	nf
0	8	0
1	2	2
2	1	2
3	1	3
7	1	7
31	1	31
40	1	40

$q = 15$ $N = 85$
$I_\delta = 5.32$
$F_0 = 26.93$
$p < .01$

Piscadera Baai Channel

n	f	nf
0	18	0
1	5	5
2	2	4
3	4	12
7	1	7
9	1	9
10	1	10

$q = 32$ $N = 47$
$I_\delta = 3.42$
$F_0 = 4.58$
$p < .01$

Carmabi #2

n	f	nf
0	29	0
1	16	16
2	1	2
3	1	3
8	1	8

$q = 48$ $N = 29$
$I_\delta = 3.78$
$F_0 = 2.66$
$p < .01$

LABORATORY DISTRIBUTIONS OF *Pagurus miamensis*

	I_δ	F_0	p
09.00 March 20	1.28	2.08	$< .01$
15.45 March 20	1.38	2.74	$< .01$
21.45 March 20	1.13	1.78	$= .03$
08.45 March 21	1.40	1.93	$< .01$

markedly after dislodging-shaking. An individual does not always show this behavior pattern when another crab crawls over it, and it is not as noticeable in *Pagurus miamensis* as in some other species. A series of experiments concerning one of the factors of stimulation of this pattern will be described in a later section.

The ambulatory raise of *Pagurus miamensis* is an upward movement of the limb through only 30°, to a position about 25° below the horizontal. In the fully raised attitude, the limb is not straight, but rather the dactyl is inclined downward slightly. The crab may raise both ambulatories simultaneously and may hold the limbs in the raised posture for several seconds. In addition to this stereotyped display, interacting crabs occasionally strike at each other with an upward then forward-down movement of an ambulatory. This pattern was only rarely seen.

Movements of the chelipeds were not as frequent as those of the ambulatories, but appeared to be more important in aggressive interactions. In 1,050 interactions, 331 cheliped extensions and 189 cheliped presentations occurred as compared with 696 raises. The crab may bring its cheliped(s) forward, as it raises its body slightly, to a position in which the dactyl(s) is at an angle of about 85–80° with the substratum. The position of the dactyl is a bit further forward than in the cheliped presentation position of diogenid crabs. The motion takes only about 0.18 seconds. Because pagurid crabs generally carry their cheliped dactyls (particularly the major) doubled back under the mouth region, the movement to the presentation position moves the dactyl through 45–60°. The cheliped extension is also a rather rapid motion of one or both limbs. The minor cheliped is moved forward and upward to a position just below the horizontal. The major cheliped is moved through 115°, to a position about 20° below the horizontal. The dactyl of the major cheliped is slightly open as the appendage is moved and held in the extended position. Occasionally the movements of a double cheliped extension are combined with a rapid forward movement of the whole body. The movement of the body appears to intensify or emphasize the motion of the chelipeds.

On just one occasion, a peculiar sequence of behavior was observed. Two large individuals had moved to within six mm of each other and were facing one another directly. They exchanged double cheliped extensions and a series of double ambulatory raises. Both were holding their chelipeds in the extended position when they began "bowing" to each other. With the chelipeds extended, first one crab and then the other would come partially out of its shell, move its body slightly down and forward and then pull back into its shell to the normal position. The two crabs bowed to each other about five times, then both moved back, turned and moved away. The significance of this dignified exchange is unknown.

Shell-fighting in pagurid crabs includes a behavior pattern not seen in diogenid crabs. Also there is somewhat less positioning behavior at the beginning of an interaction. In pagurid crabs such as *Pagurus miamensis*, the opposed position during shell-fighting behavior is slightly different from that of the diogenid crabs. The apertures of the combatants are not over one another; the shell of the aggressor barely overlaps the edge of the shell of the defender when viewed from the side. In this offset opposed position, the attacker goes through the aggressive sequence. This includes two main elements of behavior – rapping movements and spasmodic shaking. Spasmodic shaking is a series of 4–6 cycles of short movements (about one mm). The shell of the defending crab is moved back and forth along an axis parallel to the substratum and the body axis of the attacker, and perpendicular to the columella axis of the crab being shaken. The movement is brought about by a to and fro motion of the aggressor's ambulatories. The chelipeds of the attacker are stationary, resting either just in the aperture of the defending crab or on the rim of the shell-hole. The movement can also be effected by a motion of the aggressor's whole cephalothorax, everything moving except the aggressor's shell. A series of spasmodic shaking movements lasts less than a second.

Following or between series of spasmodic shaking, the attacker may go through positioning behavior. It moves the defending crab back and forth (about 30° movement) around an axis perpendicular to and through the plane of the shell aperture. Intermixed with this movement is a shifting from the left to the right ambulatories by the attacking crab. This side-to-side movement is similar to the positioning of many diogenid crabs but without any noticeable vertical motion. After this, additional series of spasmodic shaking or rapping may occur. Rapping movements are similar to those of *Clibanarus tricolor* although rarely moving over half the length of the cephalothorax and appear to be slow (about 0.75 seconds per cycle). The rapping motions are effected by two distinct types of movements. The usual rap, as described for diogenids, a second manner or rapping which is an exaggerated shaking movement. The motion is similar in the two cases, but the attacker's shell is moved in the former case and the defender's shell in the latter. Short raps may give way to spasmodic shaking without any interruption.

In a successful fight, as the defender starts to come out, he or she can be seen to tap at the mouth area of the winner with its chelipeds. Spasmodic shaking almost invariably precedes evacuation. If the aggressor is rapping as the loser starts to come out, the former moves back into the offset opposed position and performs spasmodic shaking. Some shell-fights are carried to completion without any rapping movements. There is usually no contact at all between crabs as the loser vacates its shell.

The sexual behavior of *Pagurus miamensis* includes a type of behavior pattern not seen among the diogenid crabs. After contacting a female which is about to or has recently moulted, the male turns her over into an opposed position and carries out some short rocking movements similar to the gentle rocking of *Clibanarius tricolor*. Accompanying these movements he places his chelipeds into the female aperture. He may then perform no more overt behaviors, but either holds the female quietly in his ambulatories or, more frequently, he grasps the rim of her shell aperture with either (usually major) cheliped. He may maintain this position for several hours during which time he moves about quite readily, dragging the female after him. After some minutes or hours, he may again start to rock the shell of the female and investigate the female shell aperture. He continues rocking and moving his chelipeds about in the aperture until he secures one of the female's appendages with one of his chelipeds. Although almost all combinations of limb grasped and cheliped grasping have been observed, the most frequent arrangement was the major cheliped holding the first left ambulatory of the female by the propodal segment.

After the male has attained this position, the major element of precopulatory behavior begins. The male jerks the female toward him by short rapid movements of his cheliped. These back and forth movements cover a distance about equal to the length of the eyestalks. The inward motion (pulling the female toward the male) takes 0.06 seconds (or less) and the female is held in for about 0.80 seconds, then pushed back in about 0.12 seconds. These short jerks are carried out in series of 2–6 cycles. During these movements the female is in a normal, upright position. The male may drag the female about over the bottom while holding onto her appendage. After some minutes to hours of this jerking behavior, the male turns the female over either completely onto her back or to a position, in which the plane of her shell aperture is vertical. He continues jerking and occasionally rocking the female gently for a short time. The female eventually comes up and moves her minor cheliped about in the area of the male eyestalks. The male often then releases the appendage of the female as he eases forward although he may hold on, doubling back the dactyl of the cheliped concerned

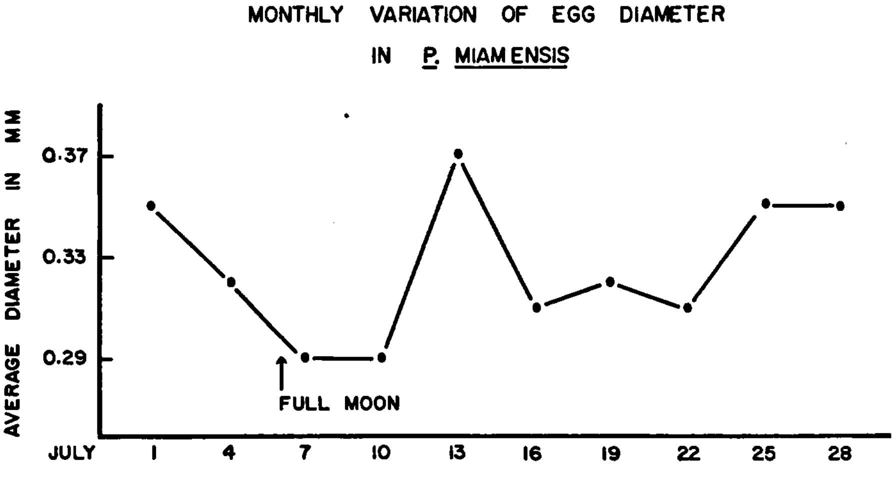


Fig. 21. Variation in average egg diameter in *Pagurus miamensis* during May, 1964.

as he gets into position. The copulatory position is as in other species and the fifth pereiopods of the male can be seen moving back and forth between the genital orifices. In eight cases, copulation lasted 3–4 seconds and in a single case it lasted 24 seconds. Occasionally just after copulation, a female moved her body in and out of her shell rapidly, as if rapping by herself.

After copulation the male often pushes the female away without any further behaviors. Sometimes the male does carry out some jerking (while holding onto either an appendage or the rim of the aperture) and rocking-rotating movements for a few minutes. When the female is released by the male, she usually has a soft exoskeleton (from her recent moult) and may have some eggs in place on her pleopods. The new eggs are rapidly brought out and attached to the pleopods. Two females had some eggs in place only two minutes after copulation. In one case, spermatophore filaments were present not only on her ventral surface but also among the new egg masses. In another instance, a large number of new eggs were in place 15 minutes after copulation – ten minutes after being released by the male. One pair was observed to mate and copulate before the female

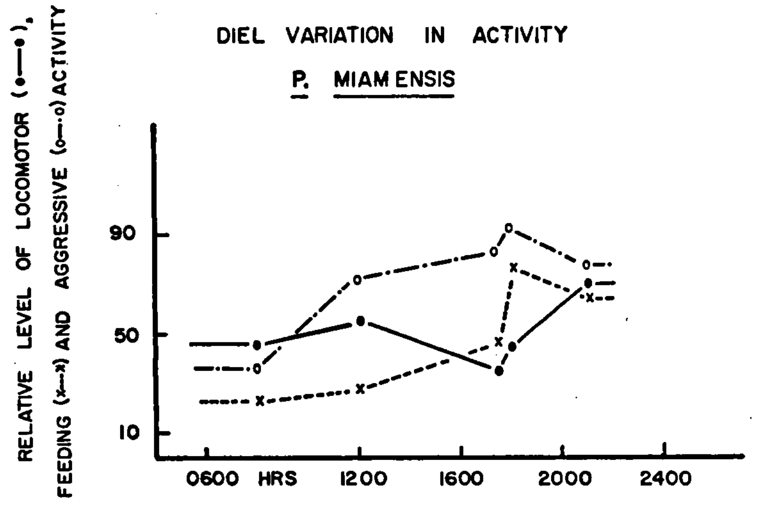


Fig. 22. Diel variation in activities of *Pagurus miamensis*. All activities generally nocturnal.

had moulted or released her old larvae. In mated pairs, the male was 0–60% larger in c.l. than the female (average 30%).

Collections and measurement of egg diameters were carried out as in *C. tricolor*. The results are shown in Figure 21. The results offer little or no support for the existence of a simple lunar cycle.

The diel variation in locomotor activity and feeding behavior measured in the laboratory is shown in Figure 22. The afternoon observations were carried out one half hour earlier than in the other species. However, the 17.00–17.30 and 17.30–18.00 hrs periods may have been too late to catch any increase in movement associated with the afternoon emigration.

Pagurus pygmaeus (Bouvier, 1918)

(Family Paguridae)

This rare species was found on Curaçao only in a few restricted localities. A total of about 70 individuals were collected. Only two specimens of this species (one of them the holotype) had been collected prior to this (PROVENZANO, pers. comm.). It is a small species, however, not quite as small as *Pagurus miamensis*, averaging about 3.5 mm in c.l. The previously undescribed color pattern is very striking. The antennules are light, transparent blue; the antennae faintly purple with white bands; eyestalks clear; cephalothorax creamish with a green tinge; chelipeds and the first two proximal segments of each walking leg a brilliant vivid scarlet (#4–D6 in MAERZ & PAUL, *A Dictionary of Color*); and the distal segments of the ambulatories are colored by sequential bands of light blue-orange-dark blue-light blue-orange-yellow-dark blue-light blue-yellow. The bands of color go completely around the legs. The tips of the cheliped dactyls are light scarlet to white. The eggs are yellow-orange. Morphologically *Pagurus pygmaeus* is more closely related to *P. miamensis* than to any other species studied.

Specimens of *Pagurus pygmaeus* were numerous only at Boca St. Michiel. A few were found at Vaersen Baai and on one side of the entrance to Piscadera Baai. This species is limited to waters with open circulation. More restrictive is the apparent requirement for an aggregate of medium to large rocks, with space between them and covered with a heavy, encrusting, red-scarlet algal growth (instead of the usual brown or green algae or detritus). The crabs were found in one meter or less of water and during the day were always hidden beneath the rocks and stones. The populations at Boca St. Michiel lived mainly under some artificially constructed rock piles, built by the fishermen of that village as waterbreakers. Populations of *Pagurus miamensis* and *Pylopagurus operculatus* were present in the same micro environment.

The aggressive behavior patterns of *Pagurus pygmaeus* rather closely resemble those of *P. miamensis.* The ambulatory raise may involve one or both first ambulatories. The limb is raised through about 35° to a position about 25° below the horizontal. The proximal segments of the limb are actually held at an angle above the horizontal; the leg is not maintained straight but is bent in such a way that the distal segments are at the above-mentioned angle. The movement upward takes up to 0.54 seconds; the downward motion is sometimes more rapid than the upward (0.30 seconds).

The movements of the chelipeds are more frequent in aggressive interactions in *Pagurus pygmaeus.* The cheliped presentation behavior pattern is similar to that described for *P. miamensis.* The minor cheliped is extended to an almost completely horizontal position. The proximal segments of the major cheliped may be horizontal in the raised attitude; however, the dactyl is held about 35° below the horizontal. The upward motion takes 0.42–0.54 seconds. Because *pygmaeus* carries its major dactyl doubled back below the mouth area when not aggressively engaged, the dactyl is moved through about 135°.

Individuals of *Pagurus pygmaeus* often show the dislodging-shaking mentioned under *P. miamensis.* The behavior pattern appears to be similar in the two species.

Shell-fighting in *Pagurus pygmaeus* contains the same behavioral elements as other pagurid crabs although rapping movements occur more than the spasmodic shaking, which predominates in other pagurids. During positioning behavior, the aggressor rotates the defending crab back and forth rapidly about an axis perpendicular to and through the plane of the defender's aperture. After these short movements, the attacking crab begins either rapping or spasmodic shaking. Most of the rapping occurs at a rate of about 0.80 seconds per cycle. In one long series of short rapid rapping motions, an attacking crab rapped the defending crab 113 times in one minute. Although some hard rapping does occur, in which the attacker's shell is moved through a distance equal to half the length of the cephalothorax, the majority of motions are about the length of the eyestalks.

The sexual behavior of *Pagurus pygmaeus* is noticeably different from that of *P. miamensis* and other pagurid crabs. Mating activity and copulation were observed only three times. In each case copulation was achieved after less than ten minutes of precopulatory behavior. None of the jerking movements seen in *miamensis* were observed. After turning a female over into an opposed position, the male placed both chelipeds into the aperture of the female. Occasionally he held his minor cheliped still, and moved the major dactyl back and forth just inside the shell-hole, rapping the sides lightly. The most consistent and constant male behavior pattern was a series of movements of the minor cheliped inside the aperture of the female. The motions included both vertical, horizontal and diagonal elements. The vertical movements were the most marked and the male appeared to move his appendage up and down in all parts of the female aperture.

After several minutes of these cheliped movements, the female came up and began tapping alternately with her major and minor cheliped at the area just below the male's eyestalks. While the female continued the tapping motions, the male started to come out of his shell farther and grasped one of the female ambulatories with his minor cheliped and sometimes grasped another with his major. As he eased out, the male appeared to pull at the grasped limbs of the female, spreading them apart. The male sometimes then tapped at the outspread ambulatories of the female with either cheliped as the pair attained the copulatory position. Once in the copulatory position, the pair was always quiet except for the movement of the male's fifth pereiopods between the genital openings. Postcopulatory behavior on the part of the male was totally absent in one case. However, in this case the female had not moulted recently and copulation itself lasted 40 seconds. In the other two cases, in which the females were soft from recent moults, copulation lasted five seconds and was followed by elements of shell-fighting behavior by the male. This consisted of about a minute of short rapping and rotations in one case. In the other, the male first performed a peculiar behavior pattern seen only this one time. It was a type of "inverse rapping" in which the male shell was motionless while the bodies of the male and female were moved back and forth in short movements as the male pulled in and out of this shell (the male was holding a female ambulatory leg with his major cheliped). After a number of these movements, the male went through rocking-rotating movements (positioning behavior) and then true rapping behavior. After a number of raps, the female came completely out of her shell and the pair exchanged shells. In the mated pairs, the males were 8–67% larger than the females (average 30%). New eggs were not yet in place in any of the females when extracted from their shells (up to two hours after copulation) although new eggs were visible in their abdomen.

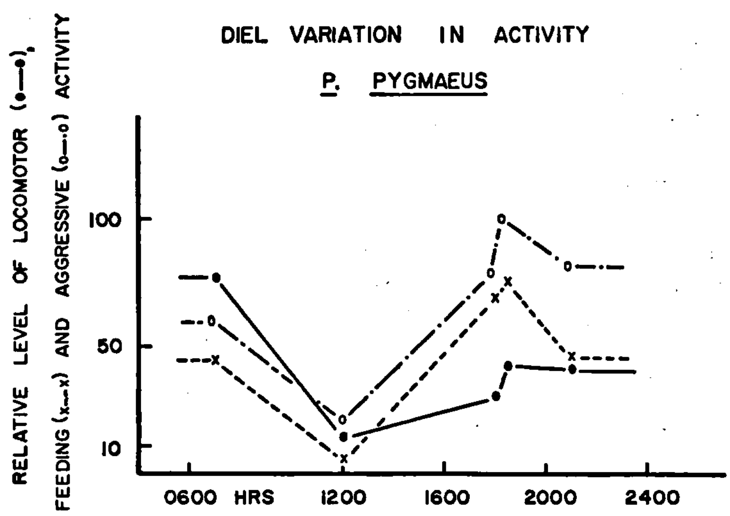


Fig. 23. Diel variation in activities of *Pagurus pygmaeus*. All activities nocturnal with crepuscular peaks.

The diel variation in activity of *Pagurus pygmaeus* was measured as in *Clibanarius tricolor*. The results are shown in Figure 23. This species is clearly nocturnal in its activity.

Pagurus bonairensis Schmitt, 1936

(Family Paguridae)

This species was one of the most ecologically limited of all those collected in Curaçao. All specimens were collected inside Piscadera Baai on shallow mudflats. Moreover, with the exception of one individual, all were found in one small section of one of the innermost inlets of that bay. *Pagurus bonairensis* is a medium-small crab, averaging about six mm in c.l.

Although *Pagurus bonairensis* may occur elsewhere in the Piscadera inner bay and in parts of other bays, I found it in a very limited area. There were two medium size populations, separated by about five meters, spread out along 20–25 meters of one side of one small indentation in the shore not too far east from the landhouse Klein Piscadera. The waters this far into Piscadera Baai are rather cloudy most of the time and it was rarely possible to see crabs in water deeper than 20 cm. The only unique feature of this particular inlet observed was the very gentle slope of the soft mud bottom which was not left dry at low tide. There are no mangroves along this particular section and the gentle slope of the bottom assures water coverage under normal circumstances. The majority of animals were found about 50 cm from shore, in water three cm deep.

At low tide, there were decidedly fewer crabs visible but the decreased visibility of the area makes any statement on tidal migration tenuous. It could not be judged whether the crab simply moved up and down with the water level (thereby staying in about the same depth of water) or if there was a real migration to deeper water during low tide. At night the problems of visibility were multiplied. During the day, especially during high tide, the crabs were rather active, moving about some and feeding. Mating pairs could frequently be seen, the male dragging the female about both during the day and at night. Around 18.00 hrs the crabs start moving generally toward deeper water (apparently irrespective of tidal factors). By 18.30 hrs there are markedly less crabs in the area. Very few individuals could be found at night. The population density appears to be at approximately diurnal level by 06.00hrs.

The table below shows the results of field distribution counts along portions of the shore at two different times. The crabs are contagiously distributed.

FIELD DISTRIBUTIONS OF *Pagurus bonairensis*

12.30 hrs July 1				06.00 hrs July 2			
n	f	nf		n	f	nf	
0	1	0		3	2	6	
1	6	6		4	1	4	
3	2	6	$I_\delta = 2.52$	5	1	5	$I_\delta = 1.33$
6	2	12	$F_0 = 6.54$	6	1	6	$F_0 = 4.92$
17	1	17	$p < .01$	7	1	7	$p < .01$
				8	1	8	
				9	1	9	
				10	1	10	
				17	1	17	
				18	1	18	
				20	2	40	
				25	1	25	

The table below shows the results of the measurement of laboratory distribution of *Pagurus bonairensis*. The laboratory populations were set up in medium-size glass aquaria externally marked every six cm. The distribution of individuals was random in the late afternoon and at night. The contagious distributions seen in the morning counts may be a result of grouping in corners of the aquarium rather than true gregariousness.

LABORATORY DISTRIBUTION OF *Pagurus bonairensis*

	I_δ	F_0	p
08.45 hrs March 23	1.45	3.82	$< .01$
16.30 hrs March 23	1.10	1.63	$> .05$
20.15 hrs March 23	1.01	1.09	$> .05$
09.30 hrs March 24	1.29	2.73	$< .01$

Pagurus bonairensis is an active, fast moving species. Although an individual may not move much while feeding in an area, its locomotion, when disturbed, is rapid. The ambulatory legs and chelipeds of this crab are relatively long and slender, and both in its speed and manner of movement *bonairensis* is somewhat spider-like. The ambulatory raise is not as frequent in aggressive meetings as movements of the chelipeds. Ambulatory raises occurred 394 times in 1,060 interactions, while 567 cheliped extensions and 291 presentations took place. The ambulatory raise is a very rapid, continuous act; the limb is not often maintained in the raised position for any length of time. It is raised through about 40° to a position slightly below the horizontal within 0.12 seconds. In the raised attitude, the dactyl is curved somewhat downward. After a short time in the fully raised position, the limb is usually brought down rapidly (0.06–0.12 seconds). The movement involves a horizontal element of about 30°; the limb is moved forward as it is raised and brought back as it is lowered.

The cheliped presentation display is similar to that of other pagurid crabs. The cheliped extension is of two types; the standard forward movement with little horizontal motion is much more frequent. The major cheliped is carried doubled back under the mouth area, and thus the major dactyl may be moved through 130°, to a position about 15° below the horizontal. The proximal segments are horizontal or even a little higher in the raised attitude. The minor cheliped is straighter and more nearly horizontal when extended. The motion upward takes 0.36–0.48 seconds and may be brought back to the neutral or presentation position just as quickly. In addition to this aggressive movement, a second cheliped movement was observed a few times. This sequence of movements brings the major cheliped out and to the side at an angle of about 45° to the anterior-posterior axis of the body. It is then moved up and back a bit further; the limb at that time being about 20° below the horizontal and 55° back from the A-P axis. It is then brought diagonally down, forward and toward the body midline to a position about 30–35° below the horizontal and 15° away from the A-P axis. It may then be brought back and the movement repeated or returned to either a neutral or presentation position. When the animal was pulled back into its shell, the major dactyl of an individual frequently was flicked upward rapidly when disturbed by another crab.

Pagurus bonairensis executes the dislodging-shaking movements typical of pagurid crabs. The motions are somewhat more rapid and violent than those of *P. miamensis*. The twisting, side-to-side action is very often successful in physically dislodging an offending conspecific individual.

Shell-fighting behavior follows the patterns for pagurid crabs. Most of the rapping motions are very short and rapid (about four cycles per second). Spasmodic shaking and rapping occur about equally during the course of shell-fights and are not too unlike in speed or distance of movement. Positioning behavior, a slow quiet rocking of the defender by the aggressor, about the axis perpendicular to and through the shell aperture of the defender, frequently occurred between series of rapping motions and/or spasmodic shaking. This rocking sometimes increased gradually in speed and changed very smoothly into spasmodic shaking.

Sexual behavior followed the typical pattern for pagurids although it occurred more frequently (36 times in 1,060 interactions) than in other species. Even though the observable populations were never large (usually less than 100 individuals in the laboratory and less than 200 visible in the field), mating pairs were almost always observable. In the field, the sight of a male holding onto or dragging a female about with his major cheliped grasping one of her first ambulatories, while both carried out feeding motions, was rather common. Occasionally a female was pulled about by a hold on the rim of the shell aperture. Either upon first encountering and attaining an opposed position with a female, or after some minutes or hours of holding a female by the aperture rim, a male rocks the female back and forth (about 30° movement) around the axis perpendicular to and through the plane of the female aperture. The male may also rotate the female back and forth about the axis parallel to the substrate and perpendicular to his anterior-posterior axis. After some minutes of these rocking movements, the female comes up partially and the male grasps one of her appendages with one of his chelipeds.

The male then may pull the female about, hold her quietly in the opposed position or hold her by an ambulatory leg while she is in an upright posture. This latter attitude usually continues for some minutes or is intermixed with short jerking movements by the grasping cheliped of the male. These movements, which pull the female toward and away from the male, are similar to those described for *Pagurus miamensis*, although they are somewhat longer (1–2) mm). After some minutes of this jerking behavior by the male, the female begins picking at the ambulatories and free cheliped of the male with her chelipeds. She continues to move her chelipeds (especially the minor) and sometimes her ambulatories over the appendages of the male and in his mouth-eyestalk region. The male eases out of his shell, exposing his cephalothorax and anterior portion of his abdomen, and bends the posterior part of his cephalothorax toward the aperture of the female. At this time his fourth and fifth pereiopods move back and forth between the male and female. However, unlike all other species obseved, the female often does not come partially out of her shell. Although the female and her behavior is obscured by the male, it appears that she remains in her shell and moves her minor cheliped back and forth rapidly between the

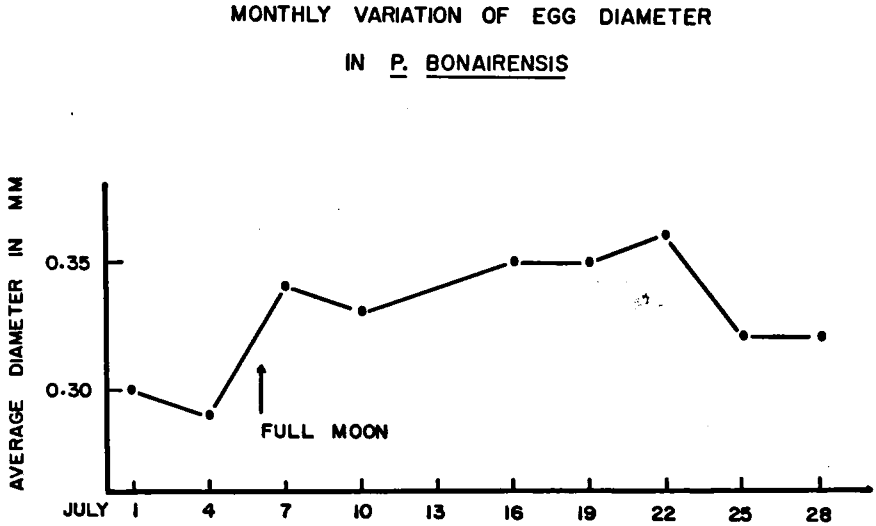


Fig. 24. Variation in average egg diameter in *Pagurus bonairensis* during May, 1963.

genital opening of the male and herself. The male is extended in this copulatory position for 5–15 seconds.

Following copulation, the male pulls back to a normal position and the female ducks down into her shell as far as the male's grasps of her ambulatory allows. The male then either releases the female and moves away or more frequently, begins to perform jerking movements again. Postcopulatory behavior is an exact repetition of the later phases of precopulatory behavior. Indeed it sometimes leads to a second or even third copulation between the same two crabs. I never observed more than three copulations by any one pair. In one case, a female mated with three different males in succession within 45 minutes. Each time, the male which had just copulated was chased away by an intruding male. In every mating observed, the female was still carrying well-developed embryos which were near the stage of release and the female exoskeleton was hard. Spermatophore filaments were almost always found around the bases of the first three pairs of female pereiopods. The

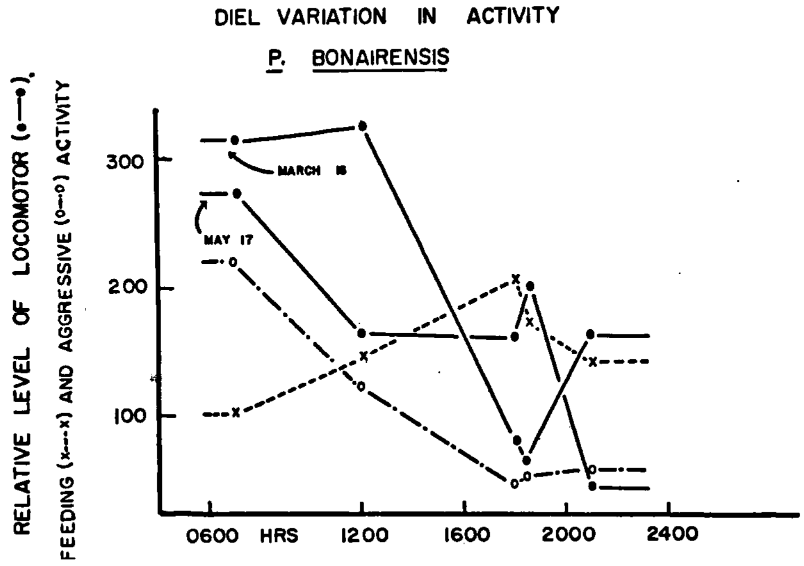


Fig. 25. Diel variation in activities of *Pagurus bonairensis*. Feeding activity shows evening peak; aggressive level shows morning peak; locomotor pattern variable two days presented separately.

males of mating pairs were 19–54% larger (c.l.) than the female (average 34%).

The results of the monthly collection and measurement of egg diameters is shown in Figure 24. From July 10 to 22, every female collected was carrying eggs externally. The variation pattern is inconclusive and the idea of a lunar synchronization is neither negated nor supported.

The diel variation in activity is shown in Figure 25. The locomotor activity figures were not averaged due to the differences between the two days of observation.

Pagurus marshi Benedict, 1901

(Family Paguridae)

This medium-size species was found at a low density level in a number of locations. It was often difficult to see due to a rather effective camouflage. The surfaces of the shell, ambulatories and chelipeds are covered by detritus material. The detritus on the shell is often held on and intermingled with hydrozoan or bryozoan colonies. The detritus material is held on the chelipeds and ambulatories by numerous long setae.

This covering was present on specimens collected in front of Carmabi, at St. Martha, Vaersen Baai, St. Kruis Baai, and Boca St. Michiel. It was much less marked in the case of those collected in parts of Piscadera Baai Channel and the entrance to Spaanse Water where the rocks are not covered by detritus matter. *Pagurus marshi* was found from about 50 cm depth down to four meters in rocky bottom, open water areas.

The table below shows the results of field distribution measurements made in two localities.

FIELD DISTRIBUTIONS OF *Pagurus marshi*

Carmabi				Piscadera Baai Channel			
n	f	nf		n	f	nf	
0	42	0		0	17	0	
1	4	4	$I_\delta = 5.33$	1	8	8	$I_\delta = 2.09$
2	1	2	$F_0 = 1.74$	2	5	10	$F_0 = 1.97$
3	1	3	$p < .01$	3	1	3	$p < .01$
				6	1	6	
$q = 48$		$N = 9$		$q = 32$		$N = 27$	

The distributions are contagious, but statistically just barely so. In the field, the crabs often seem to be randomly distributed within the area they inhabit.

Perhaps as a result of their low density level, no clear diel variation in the level of behavior was seen in the field. Individuals were observed moving about and feeding early in the morning, during the day and at night. During the evening, they seemed to be moving about and feeding somewhat less.

Pagurus marshi is a slowly moving species in general, although individuals can move rapidly at times. As in other pagurid crabs, the movements of the chelipeds are more frequent in aggressive interactions than those of the ambulatories. In 1,040 interactions, 431 ambulatory raises, 490 cheliped extensions and 263 cheliped presentations took place. The upward motion of one or both ambulatories is a rapid (0.12 seconds) movement to a position just below the horizontal. Individuals of *P. marshi*, more readily than other species, tended to perform ambulatory raises and

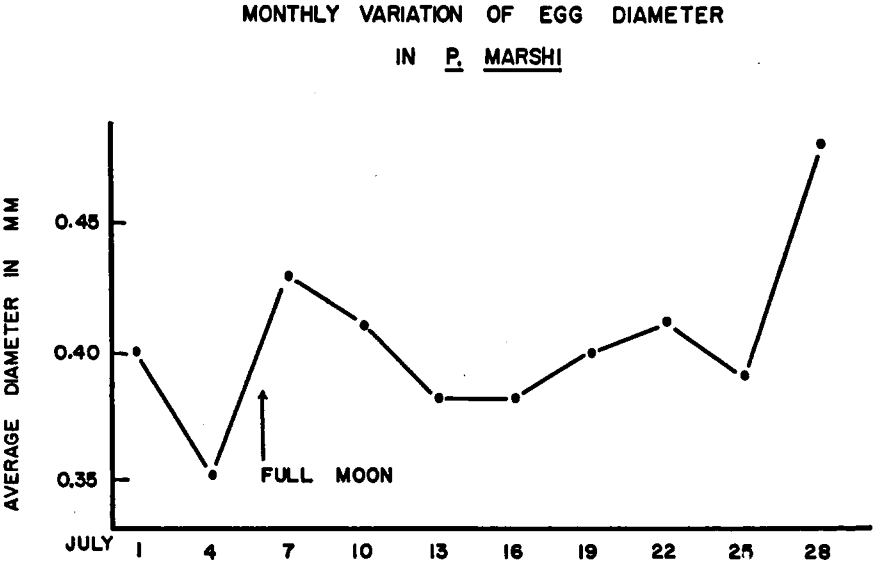


Fig. 26. Variation in average egg diameter in *Pagurus marshi* during May, 1963.

other aggressive movements toward individuals approaching from the side.

The cheliped display repertoire of *Pagurus marshi* is similar to that of *P. miamensis*. In the presentation position, the manus of the major cheliped is perpendicular to the substratum. From this position the crab may execute a major, minor or double cheliped extension. The minor cheliped is raised to about 10° below the horizontal; the major cheliped is raised to about 40° below the horizontal. Long aggressive impasses in which the major chelipeds of an interacting pair are pushed back and forth against one another are frequent. During the course of extended aggressive interactions, one or both crabs often began feeding motions. This appeared to be a displacement activity. The minor cheliped, the feeding appendage, would rapidly pick up sand grains but fail to carry most of them to the mouth appendages. The major cheliped extension of *marshi* is often executed with considerable force, and smaller individuals may be physically thrown several times their own length by a blow.

The dislodging-shaking, first mentioned in *Pagurus miamensis*, is

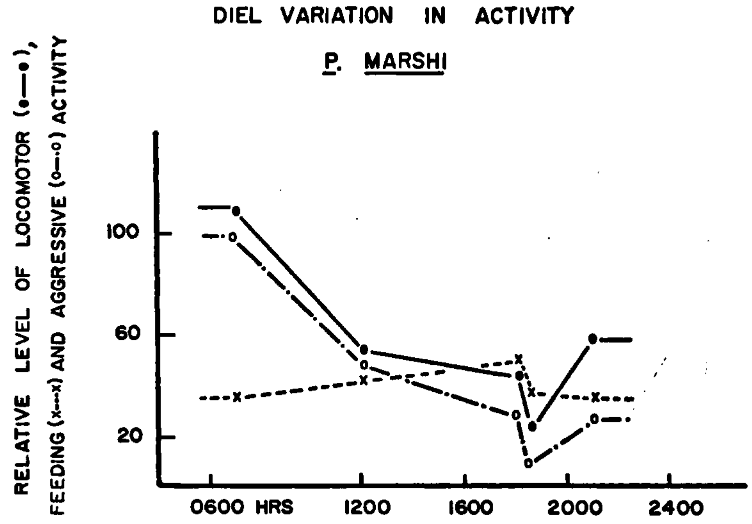


Fig. 27. Diel variation in activities of *Pagurus marshi*. Feeding level rather constant; aggressive and locomotor activity shows morning peak and evening low point.

carried out with vigor by individuals of *P. marshi*. The behavior pattern includes more vertical movements (rapidly rising onto the tips of the ambulatories) than in *miamensis*.

The shell-fighting behavior of *Pagurus marshi* follows the general pagurid pattern. Positioning moves the aggressor's body-shell through a horizontal figure 8 which includes back and forth movement, making the 8 three-dimensional. This positioning and rocking of the defender gently back and forth about the axis perpendicular to and through the plan of its aperture, precedes series of spasmodic shaking or rapping movements.

The sexual behavior of *Pagurus marshi* also follows the general pagurid pattern. A male crab may hold and pull a female for a number of hours, either by the rim of her shell aperture or one of her ambulatories. The male, while holding the female in the opposed position, moves his chelipeds back and forth in the aperture of the female. His minor cheliped is especially active in this tapping-stroking behavior. The female comes partially up after some minutes and the male grasps one of her appendages with one of his chelipeds. The male then pulls the female toward him in series of short (less than one mm) jerking motions. After some time the male gets the female in an opposed position and may continue to jerk her toward him either by his grasp of one of her ambulatories or by a movement of his ambulatories which are around her shell. In addition, he then begins tapping the outside of the rim of the aperture with his free cheliped. This light striking motion continues as the female comes up and until she is out into the copulatory position. The male may continue to tap at shell with the major dactyl during copulation. Copulation lasted 1–5 seconds. Postcopulatory behavior by the male was short or absent.

Females had recently moulted at the time of copulation however, the ecdysis process was not observed. Males do hold and pull about females that still have old larvae and have not moulted. However, all females that have been observed to copulate were found to be soft and free of larvae. The new eggs were not in place even two hours after copulation. Males were 8–89% larger than females in the mated pairs (average 50%). Although males mated repeatedly, females have been observed to mate only once.

The variation in average egg diameter during one month is shown in Figure 26. The results lend little support to the idea of lunar periodicity in mating.

The diel variation in activity in shown in Figure 27. Feeding activity is rather constant throughout the 24 hours, however the decrease in locomotor activity at dusk is rather marked.

Pylopagurus operculatus (Stimpson, 1859)

(Family Paguridae)

This medium-size species is striking in the field in both its coloration and speed of movement. The ambulatories and the minor cheliped are bright orange-red while the major manus is white and the major carpus and merus are reddish with white spots. Several specimens of a color variant were collected in which the entire major cheliped was white and the minor spotted with white. *Pylopagurus operculatus* is a very rapidly moving hermit crab. It was the only species in which specimens escaped after being observed.

Crabs were collected in open waters, with good circulation down to five meters. It was found only in areas with a substrate covered with large or medium size rocks or with coral formations containing crevices. During the day, crabs are found only under rocks or coral formations. Specimens were collected in Piscadera Baai Channel, the entrance to Spaanse Water, Vaersen Baai and Boca St. Michiel. In the artificial rock piles at St. Michiel, *Pylopagurus operculatus* generally occurred deeper within the pile than *Pagurus pygmaeus*, which in turn was generally below the main population of *Pagurus miamensis*. However, all three species did overlap and the rapid retreating ability of *operculatus* could have contributed to the depth at which it was found.

During the day, this species remains hidden from view beneath rocks and/or coral formations. Around 18.00 hrs, individuals begin to move out from beneath the rocks. As the light level decreases, these crabs (and moray eels) become more active and begin feeding. Feeding is done almost exclusively with the minor cheliped;

the much larger major cheliped is used almost solely in aggressive interactions.

The sexual behavior of the species was not observed.

The rapid locomotor ability of *Pylopagurus operculatus* mentioned above is correlated with several factors. The ambulatory legs are relatively slender and longer than those of many species. Secondly, when running, individuals of *Pylopagurus operculatus* lift their shell completely off of the substratum. This behavior. is not common in any other species observed although *Pagurus bonairensis* does do this at times.

The aggressive repertoire of *Pylopagurus operculatus* is complex in the movements of both the ambulatories and the chelipeds. The chelipeds are used more frequently in aggressive interactions.

The more common ambulatory movement is the ambulatory raise. This movement brings the appendage just about to the horizontal although the dactyl is inclined down about 15°. The movement upward, through about 45°, takes 0.24–0.30 seconds. The downward motion takes only 0.18 seconds. During this behavior pattern, the ambulatory is moved forward about 20° in rising and back while being lowered. The second type of ambulatory movement (called the ambulatory poke) occurred rarely; it was executed only five times in 1,030 interactions, in comparison with 209 standard ambulatory raises. In the execution of this behavior, the limb is raised only about 15–25° upward but is moved forward about 60° toward the eyestalk-mouth region of the other crab.

The cheliped presentation behavior pattern is similar to that of *Pagurus marshi* except that the major dactyl is not held open. The minor cheliped extension moves that appendage through an arc of a little over 90° to a horizontal position. The most common movement of the aggressive repertoire of *Pylopagurus operculatus* is the standard major cheliped extension, which occurred 563 times in 1,030 interactions. It is a very rapid, forceful movement. Crabs are often physically knocked several centimeters away by an extension. The cheliped is moved through about 140° to a position about 15° below the horizontal. The plane of the major manus in the raised position is diagonal rather than perpendicular to the sagittal plane. The upward motion takes 0.06–0.12 seconds and the limb is moved down in 0.06–0.18 seconds. The movements involved comprise the fastest aggressive display of those observed in the species studied; the complete behavior may be executed in 0.12 seconds.

During several long, intense aggressive interactions, a second type of extension movement of the major cheliped was observed. This was an "overhand-side arm" movement which tended to bring the cheliped over the other crab's cheliped when the latter was in a presentation position. The cheliped was moved forward partially, at an angle away from the midline, then raised above the horizontal. It was rapidly brought down and forward toward the eyestalk-mouth region of the other crab. Occasionally, long stand-offs occurred with both crabs pushing against the other's major manus. Displacement feeding movements sometimes occurred at such times.

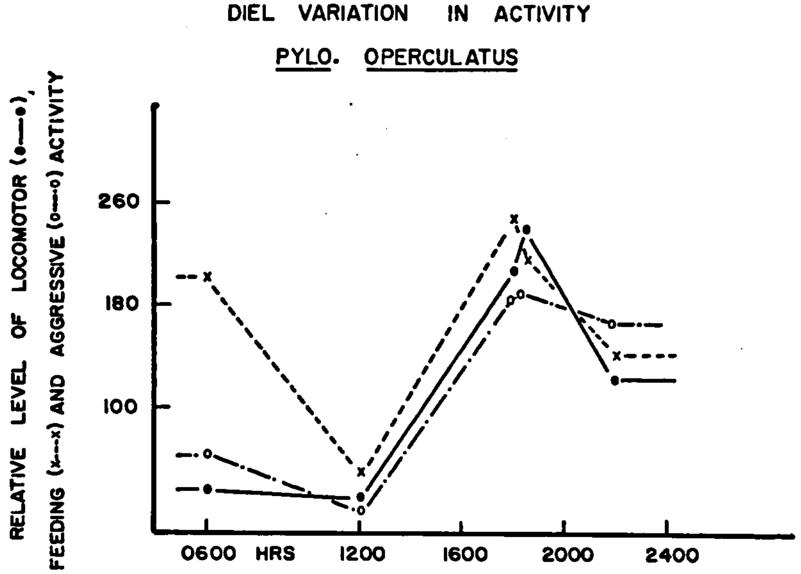


Fig. 28. Diel variation in activities of *Pylopagurus operculatus*. All activities nocturnal with crepuscular peaks.

Whenever a *Pylopagurus operculatus* pulls back into its shell, the major manus is not pulled down far but blocks the aperture near the entrance or just below. In any interaction the major manus prevents any intrusion into the shell aperture, and short rapid outward movements of the withdrawn crab's chela appear to discourage any aggressive crab.

The dislodging-shaking motions of *Pylopagurus operculatus* are more noticeable in this species than the other species observed. When one crab crawls on the back of the shell of another, the first few movements are not markedly different from the side-to-side and/or rotating motions of *Pagurus marshi*. However, if these do not dislodge the offending individual, the crawled-upon crab moves very rapidly vertically as it twists from side-to-side. This upward motion, which almost always throws the other crab off, is sometimes so violent that the behaving crab itself is thrown off the substratum and may land upside down on the sand.

The shell-fighting behavior generally follows the pagurid pattern, with an additional element introduced by the position and movement of the major cheliped. After positioning behavior, spasmodic shaking follows. However, during this the major dactyl is moved back and forth, and slightly up and down, just inside the aperture of the defending crab. These movements back and forth of the major dactyl by an attacking crab appeared to touch the major dactyl of the defender as well as the sides of the shell aperture. Movements of the major cheliped did not occur with every series of spasmodic shaking. The chelipeds of the interacting crabs do not interlock or touch as a losing crab comes out of its shell.

The diel variation in activity is shown in Figure 28. The nocturnal-crepuscular nature of the behavior patterns was maintained clearly under laboratory conditions.

EXPERIMENTAL ANALYSES OF HERMIT CRAB BEHAVIOR

AGGRESSION

DIEL VARIATION

The amount of aggressive behavior shown by any group of organisms may vary throughout the day. The diel variation of three activities has been described in earlier sections for all species studied except *Clibanarius vittatus*. The pattern of variation in aggressive activity shown by the various species, for the most part follows the variation pattern of locomotor activity. This is to be expected if the psychological aggressive level ("state") of the organism remains approximately constant. Thus with a constant level of aggressive predisposition, the variations in the number of meetings – directly proportional to locomotor activity × density (the latter remained constant in these measurements) – would produce the observed variations.

DOMINANCE ORDERS

The fact that some of the species studied maintain a degree of group solidarity in the field made the existence of more complex social arrangements seem possible. In particular, the size and apparent arrangement of the groups of *Pagurus miamensis* suggested looking for the presence of some type of dominance order. It was decided to examine groups of *Pagurus miamensis, Clibanarius tricolor* and *Calcinus tibicen* for such social structures.

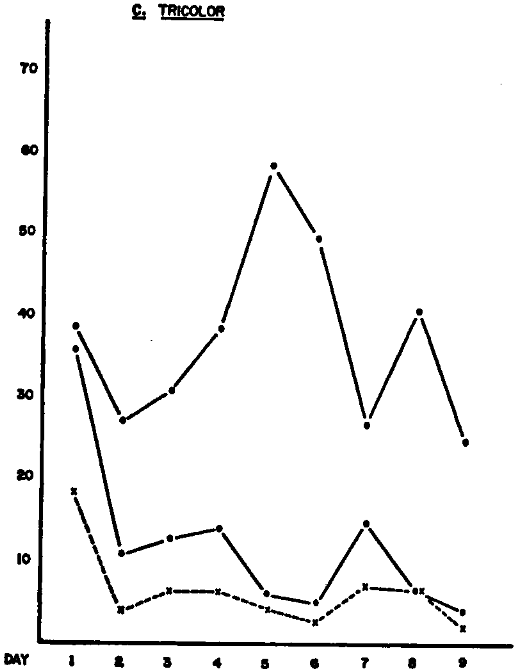
Groups of 20 individuals were established in small glass tanks with fresh sand on the bottom. The members of the group were marked on their shells with colored ink so that individual recognition was possible. Admittedly this method had the distinct disadvantage of marking the gastropod shell and not the animal itself and undetected shell changes may have contributed to incorrect observations. However, marking of the animals and, in particular, subsequent detection of any such marking was deemed highly impractical. Following removal from a storage tank and individual marking, the 20 crabs were placed in individual containers for three hours. This isolation period simply provided some degree of standardization with regard to the social interactions of the individuals just prior to the beginning of observations. That is, just before observations of its interactions with other individuals was started, every crab had the same history of aggressive interactions.

The specimens were then introduced into the observation aquarium. Five minutes later the first observation period was started. On the first day, two half-hour periods were carried out in succession. During these periods, a record was made of every aggressive interaction that took place between members of the group. In the case of the first two groups of *Clibanarius tricolor* and of *Calcinus tibicen*, observations were carried out for the next five days without any alternations. With the other three groups of these two species and the five groups of *Pagurus miamensis*, a different sequence was followed. On the fourth day, five minutes before beginning observations, the group was placed in a similar but different aquarium. This transfer simulated the change in environment that the group had experienced on initial introduction into the first aquarium, but without the handling involved in marking and the isolation between marking and placement in the tank. Observations were carried out on the next two days without special treatment. On the seventh day, about three hours before the observation time, the specimens were isolated following re-marking where necessary. Even when re-marking was not required, the specimen was handled and dried as if it were to be marked. After three hours of individual isolation, the group was reunited and observations carried out on that and the following two days. This gave a total of nine days and five hours of observations for each group. All groups were observed at the same time each day and all periods were in the afternoon (14.00–16.00 hrs), shortly before the species being observed normally made its daily migration, i.e. when the crabs were more active. After the ninth day, the size of shell (length from base to apex), length of cephalothorax and sex of every member of the group was determined.

It was assumed that the amount of aggression shown by a group, in the laboratory or field, would decrease over a period of days as some kind of stabilization was effected. This stabilization could be established by either the development of some social order or some manner of physiological-psychological fatigue. Figures 29, 30 and 31 show the variation in aggression in the three species studied over the period the groups were observed. The graphs show the averaged figures for five groups in *Pagurus miamensis* and three groups in *Clibanarius tricolor* and *Calcinus tibicen.* The solid circle and solid line represent the number of "meaningful" aggressive interactions observed each day (interactions in which one animal

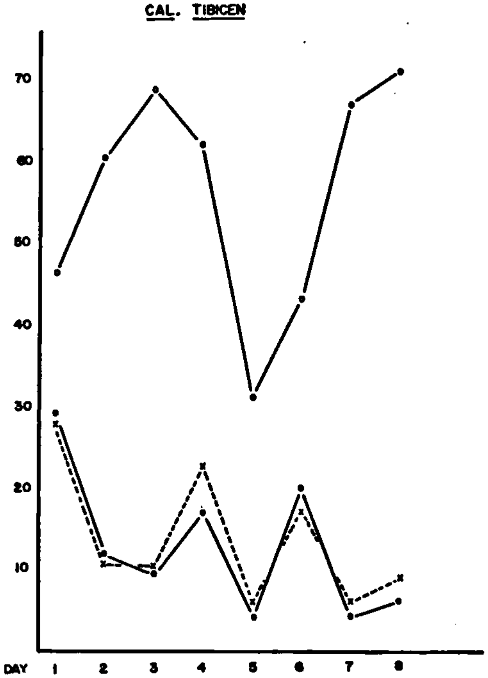
LONG TERM VARIATION IN AGGRESSION

FIG. 29



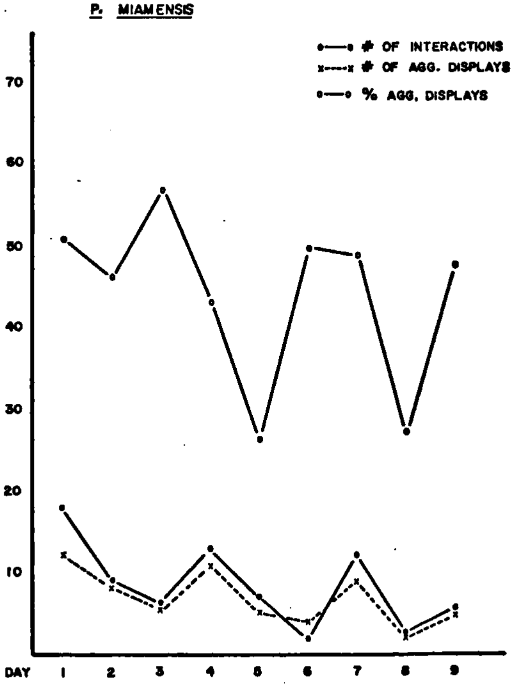
C. TRICOLOR

FIG. 30



CAL. TIBICEN

FIG. 31



P. MIAMENSIS

gave an aggressive display to the back of another were not included). The cross and dotted line represents the number of aggressive displays given by members of the group during the observation period of each day. The open circle and solid line represents the percent of meaningful interactions in which an aggressive display was given by one or both of the interacting pair.

In all three species, the pattern of variation in the aggression of the group is similar. The number of meaningful interactions and the number of aggressive displays decreased during the first three days. They then increased upon introduction into the new tank – although not to a level as high as that of the initial day of observation – and decreased even more rapidly until the second alteration (re-marking-isolation). This was followed by a second increase in these numbers – again not as high as the first day – and a decrease on the last two days. The percentage of meaningful interactions in which aggressive displays appeared was rather variable over the full period of observation and showed no consistent pattern.

In addition to this consideration of the variation in the aggression of the whole group, the data were examined for the presence of any type of dominance order. Since each shell was marked individually, it was possible to record the interactions of each individual animal during the observation periods. Whenever shell changes were observed (both during regular observation periods and at other times) the change in the "identity" of individuals was recorded and the data corrected. However, there were probably some undetected shell changes that have contributed to some of the "imperfections" in the dominance orders. However, it is felt that the five repetitions of the measurements in each species provided an adequate preliminary indication of the social order of these crabs.

A mathematical measurement of the presence or absence of social organization (whatever its basis) proved to be somewhat

Fig. 29–31. Variation in level of aggressive activity over nine days in groups of *Clibanarius tricolor*, *Calcinus tibicen* and *Pagurus miamensis*. Groups moved to new observation tank on fourth day and re-marked — isolated — re-introduced on seventh day.

4 P. MIAMENSIS

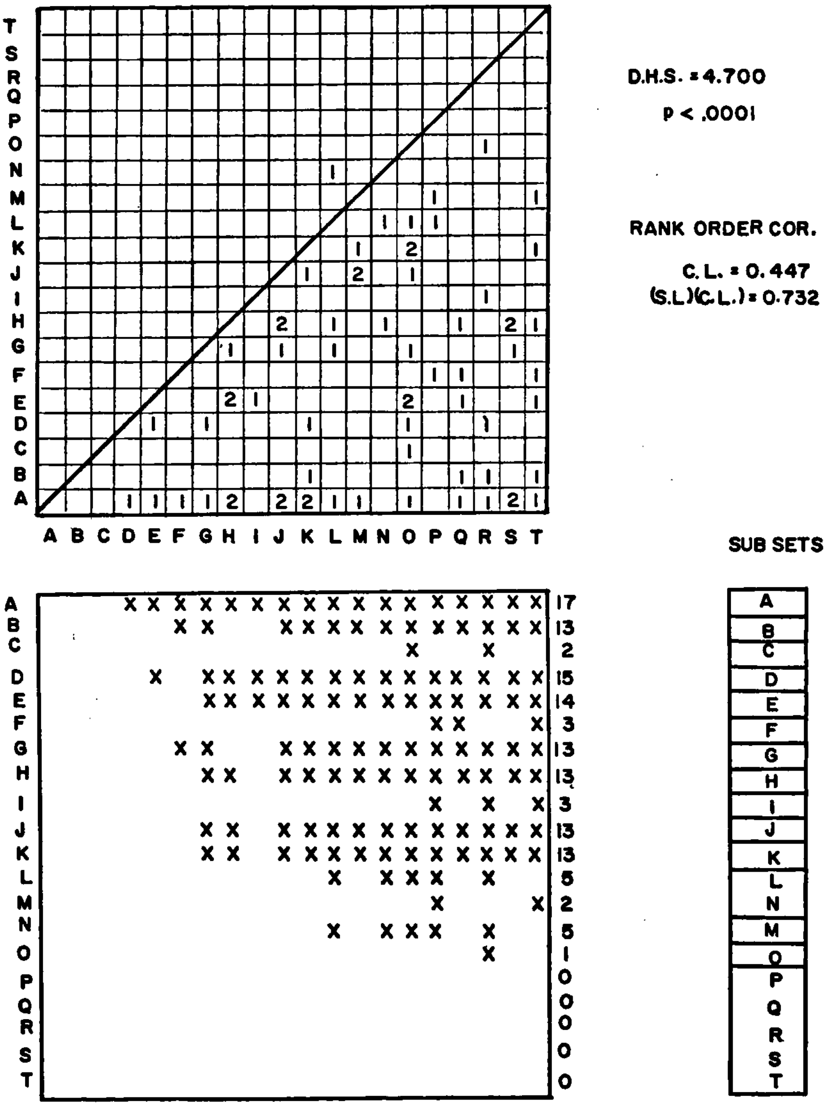
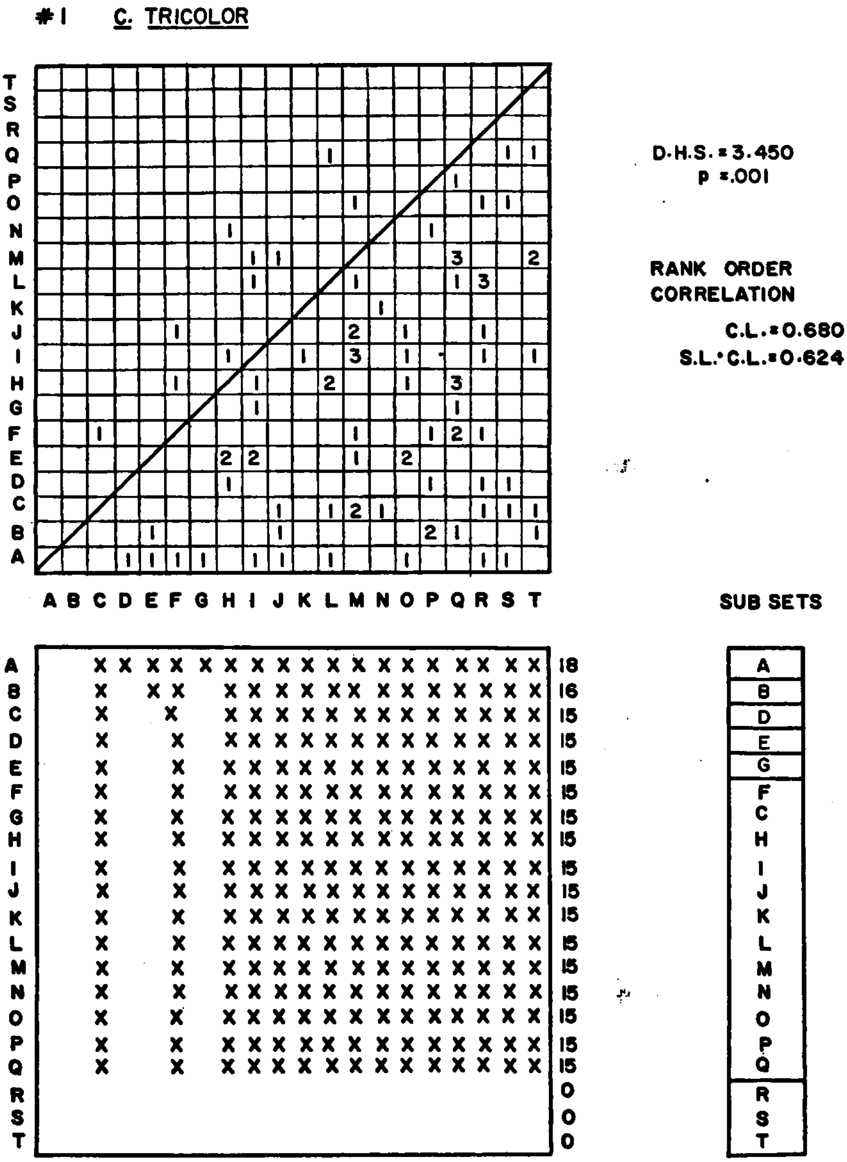


Fig. 32 Dominance order data for observation group 4 of *Pagurus miamensis*. Upper matrix shows results of aggressive interactions between members of group; dominance read across, losses read up. Dominance Hierarchy Statistic indicates amount of order in groups interactions. Lower covering matrix indicates (x) individuals over which each crab was chain-dominant. Subsets such that no individual is dominated by an individual in a lower subset.

complicated. The data were analyzed in the following manner. For each group, the interactions for all the observation periods were considered together. It is realized that any dominance hierarchy would probably not be completely established during the first period and that it would be advisable to consider only the interactions of pairs after they have interacted at least one time. However, the number of recorded interactions between all the possible pairs in each group is small, and a large portion of these occurred on the first day. For purely pragmatic reasons it is necessary to consider all the interactions as one set.

The percentage of successful interactions was calculated for every member of each group. That is, the number of aggressive interactions in which an individual was dominant (as shown by the retreat of the other crab) was divided by the total number of interactions in which it was involved. The individuals of a group were then listed in order, according to their percent dominance. The upper matrices in Figures 32, 33 and 34 show the results of aggressive interaction among the individuals of three of the groups. Interaction dominance is read across the matrix and losses are read up. If the groups showed perfect, straight-line dominance (and assuming that ranking by percent dominance was the correct ordering procedure), the results of all the fights would appear in the lower right half of the matrix – below the diagonal line. For example in group 4 of *P. miamensis* all the interactions are in the lower right half of the matrix, except one fight in which N lost to L; in another fight L lost to N.

The list of the individuals to the right of the lower matrix and the subsets into which the list is divided, was determined by a second procedure. The subsets (and the order of the subsets) are such that no individual lost directly to an individual in a lower subset. In a straightline dominance hierarchy, each subset would contain only one individual and the number of subsets would equal the number of individuals in the group. If the groups' aggressive interrelationships were completely at random (unlikely in any group, irrespective of the presence of social order, due to the many physical differences between individuals), the subset would contain all the individuals of the group. Thus the number of



D·H.S. = 3.450
p = .001

RANK ORDER CORRELATION

C.L. = 0.680
S.L.·C.L. = 0.624

Fig. 33. Dominance order data for observation group 1 of *Clibanarius tricolor*.

#1 CAL. TIBICEN

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T
T																		1		
S										1										
R				1			1													
Q														1						
P									1						1				1	
O																				2
N			1									3				1		1		
M				1	1		1							2				1		
L							1	1	1				1	2	1		3			
K								1				1	2							
J																1	1		1	
I			1				1			1		2						1	1	
H				1	1				1			1		1	1					
G													3	1					1	1
F													1						1	
E								1	1									1	1	
D								1	1		1							1		
C											2	2						4		
B			2				6			1	1		1			2			1	
A		2				1	2		1		1	3	1	2		3		1		2

D.H.S. = 2.060
P = .04

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	
A		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	19
B			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	17
C			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	17
D			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	17
E			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	17
F			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	17
G			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	17
H			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	17
I			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	17
J			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	17
K			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	17
L			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	17
M			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	17
N			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	17
O			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	17
P			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	17
Q			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	17
R			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	17
S			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	17
T			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	17

SUB SETS

- A
- B
- F
- D
E
C
G
H
I
J
K
L
M
N ●
O
P
Q
R
S
T

Fig. 34. Dominance order data for observation group 1 of *Calcinus tibicen*.

FORTRAN PROGRAM
FOR SOCIAL ORDER ANALYSIS

```
    DIMENSION IN(20.20),L(20,20),M(20,20),N(20,20),KUM(20),TAG(20),TIT
   1LE(12)
100 READ INPUT TAPE 5,101,(TITLE(I= 1,12)
101 FORMAT (12A6)
    WRITE OUTPUT TAPE 6,101,(TITLE(I),I=1,12)
    DO 102 I=1,20
102 READ INPUT TAPE 5,103,TAG(I),(IN(I,K),K=1,20)
103 FORMAT (A6,20I1)
    DO 105 I=1,20
    DO 105 K=1,20
    IF (IN(I,K))104,104,110
104 IN(I,K)=0
    L(I,K)=0
    GO TO 105
110 L(I,K)=1
105 M(I,K)=L(I,K)
    WRITE OUTPUT TAPE 6,106
106 FORMAT(21HO I.D.    WIN MATRIX  //)
    DO 107 I=1,20
107 WRITE OUTPUT TAPE 6,14,TAG(I),(IN(I,K),K=1,20)
    WRITE OUTPUT TAPE 6,108
108 FORMAT(2HO  ///)
    DO 10 LOOP=2,20
    DO 3 I=1,20
    DO 3 K=1,20
    KTEMP=0
    DO 1 J=1,20
  1 KTEMP=KTEMP+(L(',J)*M(J,K))
    N(I,K)=0
    IF(KTEMP)3,3,2
  2 N(I,K)=1
  3 CONTINUE
    SENSE LIGHT 0
    DO 5 I=1,20
    KUM(I)=0
    DO 5 K=1,20
    KUM(I)=KUM(I)+N(I,K)
    IF(M(I,K)-N(I,K))4,5,5
  4 M(I,K)=1
    SENSE LIGHT 1
  5 CONTINUE
    IF(LCOP-2)9,6,9
  6 KOUNT=0
    NUM=0
    DO 8 I=1,20
    DO 8 K=1,20
    IF(N(I,K))8,8,7
  7 NUM=NUM+IN(I,K)=IN(K,I)
    KOUNT = KOUNT +IN(I,K)

  8 CONTINUE
  9 IF (SENSE LIGHT 1)10,11
 10 CONTINUE
    GO TO 100
 11 WRITE OUTPUT TAPE 6,12
 12 FORMAT (40H  I.D.    COVERING MATRIX    DOMINANCE    //)
    DO 13 I=1,20
 13 WRITE OUTPUT TAPE 6,14,TAG(I),(M(I,K),K=1,20),KUM(I)
 14 FORMAT(1X,A6,20'1,17)
    X=NUM
    Y=KOUNT
    Z=(Y-(X/2.))/SQRTF(X/4.)
    WRITE OUTPUT TAPE 6,15,Z
 15 FORMAT(34HO  DOMINANCE HIERARCHY STATISTIC =F5.3)
    GO TO 100
    END(1,0,0,0,0,0.1,0,0,1,0,0,0,0,0)
```

subsets into which the group can be divided could be taken as a measure of social organization. Unfortunately there are no statistical tables available to determine the probability of chance occurrence of such subset arrangements. The ranking by these subsets has been used here as the "correct" dominance order in calculating rank order correlations. The order of individuals within the subsets is not meaningful; all crabs in a subset are considered to be equal.

The D. H. S. number is the Dominance Hierarchy Statistic value for the group. This was calculated by comparing the interactions of all possible pairs in the group. In a straight-line dominance organization, if A is dominant over B and B dominant over C, A would be dominant over C (probability that A is dominant over $C = 1.00$). A null hypothesis of no dominance order was assumed; i.e. the probability that A would be dominant over $C = 0.50$. The D.H.S. presented is the number of standard deviations away from the mean of a binomial distribution of dominance probabilities, which the actual distribution of interactions presents. That is, there is a certain chance distribution of deviations from the probabilities assumed in the null hypothesis. A value of 1.96 or greater is significant ($p \leq .05$), a value of 2.58 or greater is very significant ($p \leq .01$). The probability for each distribution is given with the D.H.S. The FORTRAN program for calculating the D. H. S. of a group is shown in Figure 35.

In addition to the above data, the lower left matrix of each figure shows the distribution of direct and indirect dominance. This covering matrix indicates the individuals that each crab was dominant over either directly or indirectly. That is, if A was dominant over B and B over C, A was considered dominant over C (an × in the matrix), even if they were not observed to interact. The covering matrix includes all possible chains of interactions between all members of the group. The number to the right of each individual's row is the number of crabs it was chain-dominant over. The

Fig. 35. FORTRAN program for calculating Dominance Hierarchy Statistic and covering matrix of interactions of members of a group.

TABLE 6

DOMINANCE ORDER STATISTICS

				Rank Order Cor.i	
	D.H.S.	p	#Subsets	c.l.	s.l. × c.l.
#1 *Pagurus miamensis*	4.131	.0001	8	0.628	0.645
#2 *Pagurus miamensis*	2.967	.004	8	0.650	0.644
#3 *Pagurus miamensis*	2.183	.03	4	0.560	0.500
#5 *Pagurus miamensis*	3.317	.001	10	0.765	0.668
	3.459 = Average D.H.S. for *P. miamensis*				
#2 *Clibanarius tricolor*	1.279	.201	2	—	—
#3 *Clibanarius tricolor*	3.442	.001	5	0.760	0.670
#4 *Clibanarius tricolor*	4.041	.0001	7	0.830	0.740
#5 *Clibanarius tricolor*	3.904	.0001	6	0.741	0.433
	3.224 = Average D.H.S. for *C. tricolor*				
#2 *Calcinus tibicen*	1.300	.194	4	—	—
#3 *Calcinus tibicen*	3.536	.0004	3	0.612	0.613
#4 *Calcinus tibicen*	2.694	.008	5	0.540	0.631
#5 *Calcinus tibicen*	4.644	.0001	9	0.702	0.541
	2.849 = Average D.H.S. for *Cal. tibicen*				

significance of these data will be discussed below. Table 6 presents the statistical data for the other groups observed.

Using the subset-determined dominance order, rank order correlations were determined for several morphological characteristics of the crabs in each group which showed some order (i.e. D. H. S. ≤ 2.58). The correlation values obtained are presented to the right of the upper matrix for each group and in Table 6. Correlations were calculated between the dominance order and a ranking by cephalothorax length (c.l.). The crabs were ordered from largest to smallest and rank order correlations calculated. A second ranking was established for each group according to an index value (s.l. × c.l.). This index was obtained by multiplying the length of the cephalothorax of each crab by the greatest length of the individual's shell. Where the rank order correlation value of this index is clearly larger than the c.l. value, it would appear that the size of the individuals' shells may have helped to determine their positions in the dominance order.

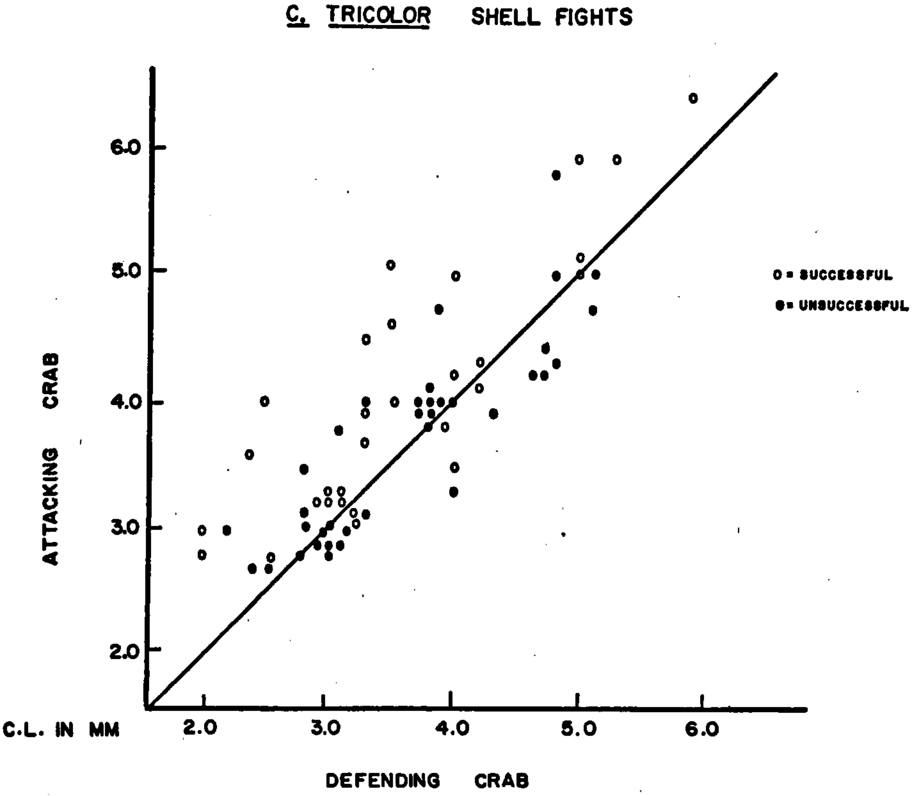


Fig. 36. Size relationship in attacking and defending crabs in shell-fights, *Clibanarius tricolor.*

Correlations were calculated to determine if the sex of an individual was important in establishing a crab's position in the dominance order. The individuals were ranked by cephalothorax length and dominance order position within each sex. That is, both the males and females were ranked by size and order within their own sex. The rank order correlations obtained for the intra-sex rankings indicated that sex is not important in determining an individual's position in the social order. For example, the non-sex-restricted (c.l.) rank correlation value for group 5 *Pagurus miamensis* is 0.76 while the average for the intra-sex ranking correlations is 0.44.

It is believed that the lower value for this correlation is due to the small number of individuals involved and the resulting increase in chance deviations. In all groups of *P. miamensis*, the intra-sex correlation values are slightly lower than the standard c.l. rank correlation values. The values for the *Clibanarius tricolor* and *Calcinus tibicen* groups are the same or very slightly higher than the c.l. rank correlation values.

SHELL-FIGHTING

In addition to the observations on general aggressive behavior, some quantitative data were gathered concerning shell-fighting behavior. This phenomenon was described above under the various species as observed in both natural and artificial shells. The relatively few interactions recorded for species other than *Clibanarius tricolor* will not be considered here. Fights were observed at various times both in 1962 and 1963. When possible, the fighting individuals were removed after they had completed their interaction and they were measured, sexed and usually their exoskeleton condition was judged. The latter datum was not systematically checked in early observations but in the majority of the interactions recorded, the exoskeletons were checked to see if one of the individuals had shed recently.

The size relationships between interacting individuals of *Clibanarius tricolor* is shown in Figure 36. Of the 66 fights represented, 30 were successful (attacking individual did extract the defending individual) and 36 were unsuccessful (attacking individual did not extract defending crab, gave up and moved away from the defending crab).

Among the successful fights, the winner was smaller than the loser in only five. One of these was a very early measurement of 1962 (the winner was 0.5 mm smaller) and may not be very accurate since a simple straight rule was then employed instead of the calipers used in the great majority of the measurements. Also, the shell condition of the loser was not determined in this case. In the other four cases, the loser was just 0.1 mm larger than the winner. In addition, three of these involved losers that had recently shed. Thus there was just one clear case out of 30 in which a smaller crab extracted a larger normal individual.

In the 30 successful fights, the winner averaged 0.45 mm larger than the loser. The greatest size difference in any case was 1.6 mm. Of the 36 unsuccessful fights, the attacking individual was larger in 22 cases (greatest difference 1.00 mm) and smaller in 14 cases (greatest difference 0.7 mm). The attacker averaged 0.1 mm larger.

Of the 54 fights in which care was taken to check exoskeleton conditions, the defending individual was soft (had shed recently) in twelve. A sample of 50 individuals of *Clibanarius tricolor*, chosen at random from a storage tank contained three soft individuals. A two-by-two contingency test of these data gave a chi-square value of 5.56 ($p < .02$). Thus individuals that have recently shed are more subject to attack. Moreover, soft individuals tend to lose to smaller individuals than normal crabs. A t-test value of 5.88 ($p < .001$) was obtained by comparing the means of the size differences in successful fights (average difference in c.l. = 0.04 mm when the defending crab was soft, 0.55 mm when normal). Thus a crab which has recently moulted, is more likely to be attacked and much more likely to lose when attacked.

The sex of the interacting individuals appears to be only of minor importance. In cases in which the attacking individual was female and the defending was a male, the average size difference were 0.25 and 0.13 mm for the successful and unsuccessful fights respectively. When the attacker was male and defender was female, the averages were 0.72 and 0.02 mm. It would appear that a male must be larger than a female to win (or defend successfully) in a shell fight. Comparing the mean size differences of the two classes of heterosexual interactions, a t-test value of 2.15 ($0.10 > p > 0.05$) was obtained. This indicated that although males that had won over females were on the average larger than females that had won over males, the standard deviations were such that the means are not statistically different. However, the t-test value is very close to a $p = .05$ level, indicating a slight (but not significant) difference, i.e. females almost have an advantage in shell-fights over males of the same size. The same situation may be true in the interactions of *Calcinus laevimanus* (REESE 1962b).

ANALYSES OF STIMULI

VISUAL STIMULI

Observations of the social interactions of these pagurids led me to consider certain movements and positions as possible elements of the communications systems of these crabs. But observations of interactions alone, however consistent as to sequence, cannot establish the stimulus value of any physical cue. A number of experiments were carried out in an attempt to prove that the observed physical changes are effective stimuli in the behavior of these crabs.

The behaviors which were observed most extensively were, of course, visual movements and postures, since these are the easiest for a human observer to sense. Certain movements and positions of the chelipeds and ambulatory legs were described in earlier sections. In order to test the hypothesis that these postures are indeed visual stimuli, series of model presentations were carried out with a number of the species studied.

Following initial failure with artificial "legs", experiments incorporating models fashioned from the exoskeletons of individuals of the species being tested, were carried out.

The test and control models were obtained by choosing several approximately equal, medium-size individuals of the species, killing them and placing the cephalothorax and attached appendages in the desired positions to dry. Normally moulted exoskeletons were used for some models in *Clibanarius cubensis* and *Paguristes grayi*. The chelipeds and ambulatory legs were held in either neutral (normal walking, etc.) or test (aggressive display) positions by bits of clay and/or cork. After 24 hours, the specimens had dryed, and their limbs were relatively fixed in position. The entire cephalothorax was then glued to the end of a glass rod 10 cm long, 4 mm in diameter. Glue was also placed around the proximal joints of the appendages to add rigidity and maintain limb position. After an additional 24 hours, the models were ready for use except in those cases where alteration of the normal color pattern was carried out. In each case, the test model was an exoskeleton, the limbs of which were arranged in the raised or extended position of an aggressive display. The control model was an exoskeleton of the same size whose limbs were in a neutral position.

In the case of *Calcinus tibicen* and *Clibanarius tricolor*, tests were carried out to measure any possible stimulus value of the white tips of their chelipeds and ambulatories. For this, additional aggressive models, with the white tips of their limbs colored the same color as the rest of the limb, were used and the reactions compared with those shown to normally colored aggressive models.

Test and control models for each display were presented individually to 50 crabs in each species. The sequence of test-control presentation was constantly varied. Every individual was tested only once with each stimulus-control set of models. The individual to be tested was placed in the test container and, after the crab had adjusted to the container sufficiently to be moving about, the models were presented to it one at a time. Each model was moved in front of the organism being tested to within a distance approximately equal to the total length of an individual of that species. The distance of model presentation varied from species to species but was held constant for each species. Every effort was made to present the test and control model in an equal manner. The movement of presentation was slow and even in all cases; such that it was judged that the crabs were reacting to the position of the model's appendages and not its overall movement. The model was held quietly in front of the test animal for three seconds and then removed; the reactions of the individuals to the models were recorded. These reactions are listed in Tables 7 and 8. Two-by-two contingency tests were calculated to see if the reaction classes "aggression", "aggression-with-retreat" and "retreat" are statistically of the same population of reactions. In all but two cases, this was true, i.e. all active reactions shown to the models could be regarded as one set. The reactions shown to the test and control models were then compared with the "nothing" (no reaction) class using chi-square tests.

In addition to these static model tests, one series of presentations was carried out with a model in which motion of the limb could be controlled by the experimenter. In this experiment, two wooden and glass apparatus were fashioned in which a major cheliped from a specimen of *Calcinus tibicen* could be placed and moved upward in an approximation of the motion of a cheliped extension display. Control and test models (with motion) were presented to 50 *Cal. tibicen*. There was no statistical difference between the behavior patterns shown toward the cheliped extension with motion and those shown toward the test model in the static series.

As can be seen from the results of the model presentations, the position of the appendages can act as stimuli (sensu stricto) in the aggressive behavior of these species. On the basis of the contingency tests, almost all reaction classes were lumped and tested against the "nothing" class for each display. This was not done for the tests of the ambulatory raise in *Pagurus bonairensis* and *Calcinus tibicen,* since the crabs had shown a considerable amount of aggression toward the control model in both cases. In these instances, the chi-square tests were calculated using the distribution of "retreat" and "nothing" reactions to the test and control models. In every case, the chi-square values are very significant.

The tests designed to determine the importance of the white tips of the appendages in the behavior of two species yielded mixed

TABLE 7

REACTIONS TO STATIC MODELS BY DIOGENID CRABS

	Calcinus tibicen					*C. tricolor*			*C. cubensis*				*Pts. grayi*		
	Con.	C.E. d	C.E. n	Con.	A.R.	Con.	A.R. d	A.R. n	Con.	A.R.	Con.	C.E.	Con.	A.R.	C.E.
(1) Retreat	7	23	28	9	20	16	25	38	18	38	25	39	4	22	18
(2) Retreat& Agg.	0	1	1	0	0	0	0	2	0	1	0	1	1	0	1
(3) Aggression	8	9	9	5	12	0	2	0	1	0	0	0	1	8	6
Nothing	35	17	12	36	18	34	23	10	21	11	25	10	44	20	25
Chi^2 1–2	0.301 $p > .50$								0.47 $p < .50$		0.91 $p > .30$		4.56 $p < .05$		0.83 $p > .30$
Chi^2 1–3				0.01 $p > .90$		1.24 $p > .20$		0.83 $p > .30$							
Chi^2 1 & 2–3	3.06 $p > .05$	4.34 $p < .05$							2.53 $p > .10$				0.26 $p > .50$		0.15 $p > .70$
Chi^2 R–N	12.98 $p < .01$	21.38 $p < .01$		13.04 $p < .01$		5.12 $p > .02$		23.37 $p < .01$	16.42 $p < .01$		9.90 $p < .01$		25.00 $p < .01$		16.90 $p < .01$
Chi^2 T_n–T_c		1.21 $p > .20$					5.86 $p > 02$								

TABLE 8

REACTIONS TO STATIC MODELS BY PAGURID CRABS

	Pagurus marshi				*P. miamensis*				*P. bonairensis*				*Pylo. opercul.*		
	Con.	A.R.	Con.	C.E.	Con.	C.E.	Con.	A.R.	Con.	C.E.	Con.	A.R.	Con.	A.R.	C.E.
(1) Retreat	13	28	16	35	10	28	14	23	9	19	4	14	13	30	35
(2) Retreat & Agg.	0	4	0	3	1	6	1	5	0	4	0	2	0	0	2
(3) Aggression	0	0	1	2	3	3	1	3	6	13	16	13	1	0	1
Nothing	37	18	33	10	36	13	34	19	35	14	30	21	36	20	12
Chi^2 1–2	0.178		1.30		0.46		1.02		2.78		0.55		1.40		
	$p > .50$		$p < .30$		$p > .50$		$p > .30$		$p > .05$		$p > .50$		$p < .25$		
Chi^2 1–3											6.07				
											$p > .01$				
Chi^2 1 & 2–3			0.02		0.14		0.16		0.07				0.19		
			$p > .80$		$p > .70$		$p > .50$		$p > .80$				$p > .50$		
Chi^2 R–N	14.59		21.30		21.19		9.00		17.77		8.69		11.27		24.20
	$p < .01$		$p < .01$		$p < .01$		$p < .01$		$p < .01$		$p < .01$		$p < .01$		$p < .01$

results. The distributions of reactions shown to the models with the white tips colored were not very different from the distributions shown to the "aggressive" models with normally colored appendages. In both *Calcinus tibicen and Clibanarius tricolor,* the reactions shown to the colored-appendage models were statistically different from the reactions to the control model. However, in *Cal. tibicen* these were not different from those shown to the normally colored cheliped extension model (chi-square = 1.214, $p > .20$). Thus it would appear that the white tips of the chelipeds are not visual aggressive stimuli. In *C. tricolor,* the aggressive stimulus value of the ambulatory raise display was significantly decreased by the elimination of the white tips of the ambulatories. The difference in the reactions shown to the two test models is significant (chi-square = 5.86, $p < .02$). Thus the white tips on the ambulatories of *C. tricolor* do act as aggressive stimuli.

If the chi-square values for the differences in the test and control sets of reactions are accepted as a measure of the stimulus value, the relative importance to the crabs of these limb positions may be judged. In *Calcinus tibicen,* the cheliped extension is a stronger stimulus ($chi^2 = 24.17$) than the ambulatory raise ($chi^2 = 13.04$). However, in *Clibanarius tricolor,* the ambulatory raise is a strong stimulus ($chi^2 = 23.37$). As with *C. tricolor,* the ambulatory raise is a stronger stimulus than the cheliped extension in *Clibanarius cubensis* and *Paguristes grayi.* In all the pagurid crabs tested, the cheliped extension was a stronger stimulus than the ambulatory raise. The ambulatory raise in *Pagurus bonairensis* had the lowest value for any normally colored posture tested ($chi^2 = 8.69$), while the reactions of *Pylopagurus operculatus* to the cheliped extension model were the strongest shown ($chi^2 = 24.20$). Also of interest is the difference in the number of times that aggressive behavior was shown toward all models by individuals of *Calcinus tibicen, Paguristes grayi* and *Pagurus bonairensis,* as compared to the few shown by *Clibanarius tricolor* and all other species.

In another series of presentations concerned with the analysis of visual stimuli in these hermit crabs, the reactions of individuals to the sight of a hermit crab in its shell was tested. The stimulus in this series was the sight of the crab itself, as a mirror was placed in front of the crab.

As in the model presentations, 50 or more specimens were tested individually. After the crab's adjustment to the test container, a small (5.5 × 8.0 cm) mirror was moved vertically down to a position about one cm from the crab and then held there for three seconds. The crab's reactions were recorded. The reactions shown by all the individuals of each species are listed in the table below. In some species (*Cal. tibicen*, *Clib. tricolor* and *Pag. miamensis*), individuals were tested twice. Once, after being a member of a group of conspecific individuals for a number of hours, and once, following three hours of isolation in individual containers. Pilot tests had indicated a possible difference in the reactions to the test situation depending on the individual's social environment just prior to testing. However, analysis of the data revealed no statistical difference in the reactions shown by the crabs tested after the two treatments.

Reactions to Mirror Presentation

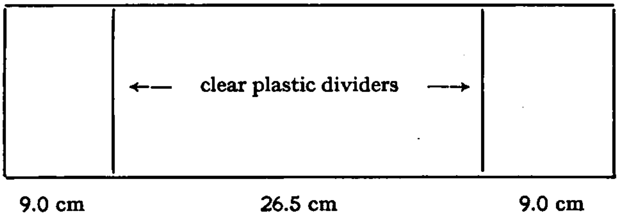
	Retreat	Retreat & Agg.	Agg.	Move Parallel	% React.	Nothing	*Total*
Calcinus tibicen	49	11	6	12	90	9	87
Clibanarius tricolor	23	6	7	16	81	12	64
Pagurus miamensis	43	5	3	1	93	4	56
Pagurus bonairensis	30	6	1	4	82	9	50
Pagurus pygmaeus	17	21	3	1	84	8	50
Pagurus marshi	17	0	0	0	34	33	50
Pylopagurus operc.	23	11	6	0	80	10	50

It can be seen that in some species, the most frequent reaction shown by the crab being tested was retreat from the image of itself. This was true with *Calcinus tibicen, Clibanarius tricolor, Pagurus miamensis, P. bonairensis* and *Pylopagurus operculatus.* Apparently the sight of a crab of the "same size" (even through in a neutral position) is sufficient to elicite retreat. The reactions to the sight of a complete crab in its shell appears to be stronger stimulus than the cephalothorax and appendages alone, such as were usid in the model presentations. Admittedly the models on glass rods were moved slowly toward the crab while the mirror (and accomdanying reflection) were presented all at once by the vertical movement involved in presentation. (This method was used to avoid creating the waves that would have been caused by any horizontal movement.)

However, the retreat reactions shown in the latter case are much more frequent than the retreats shown to the control (neutral) models in the model presentations. If equality of presentation methods could be assumed, this would indicate that a crab in a shell has a higher stimulus value than a similar crab not in a shell.

Individuals of *Pagurus marshi* tended to not react at all to the presentation of the mirror. In fact, this species' distributions of reactions in the two sets of visual test presentations (mirror and control models) are very similar. Perhaps the detritus camouflage on the shell decreases its aggressive stimulus value. Even more likely, is the possibility that individuals of this species can not judge the size of a conspecific individual (due to the camouflage) unless it executes an aggressive display. Individuals of *Pagurus pygmaeus* reacted 84% of the time and did eventually retreat 78% of the time. However, the majority of those retreats were preceded or accompanied by the execution of an aggressive display. Thus the sight of a conspecific individual evoked an aggressive reaction in *P. pygmaeus*, but initially a positive rather than a negative one.

As described in an earlier section, *Clibanarius tricolor* gathers in dense aggregations during the day. In order to see if visual stimuli play a role in the formation and/or maintanence of these groups, a series of tests were carried out. (The fact that the aggregations are formed for the most part before sunrise, made the existence of visual stimuli seem less likely.) A large enamel pan was utilized (see Figure below); the bottom was covered with sand partitioned into three sections with dividers of clear plastic. The plastic dividers were held in place with putty, making the compartments watertight.



Fifteen specimens of *Clibanarius tricolor* were placed in the right or left compartment and the individuals to be tested were placed in the center, one at a time. Their position in the pan 5, 10, 15 and 20 minutes later was noted. The test side was alternateq frequently Although this experimental method would not eliminate any possible "auditory" signals, it does eliminate the possibility of chemical cues. All tests were carried out in the morning and early afternoon. Thirty-five individuals were tested, two of which did not move during the test period. The results are shown in the table below. As can be seen, no orientation was shown, either in the total time "spent' in the two half of the middle section (represented by the number of times a crab was observed in one half or the other at the specified times) or in the initial direction of movement.

	Test side	Control	chi^2	p
Time spent	46	42	0.18	$> .75$
Initial direction	15	18	0.28	$> .50$

CHEMICAL STIMULI

As mentioned in the previous section, I wished to discover the cues which contribute to the formation and maintenance of the diurnal aggregations of *Clibanarius tricolor* and of *Pagurus miamensis*. During the course of experiments concerned with this phenomenon, several types of reactions to chemical stimuli were discovered. In the case of *C. tricolor*, two varieties of the test apparatus were employed. The apparatus used for the great majority of the tests is outlined in Figure 37. During the summer of 1962, a large enamel pan was used in place of the Y tube employed in all the 1963 tests.

A population of organisms was established in the right or left tank (test tank). This population was maintained for at least 24 hours before testing began. The rate of flow of the common water supply was maintained at about 100 cc/minute to each tank. The rates of flow from the test and control tanks were maintained at about 45 cc/minute. Although the latter rate was checked quantitatively just a few times, the two outlets were frequently checked for equality of flow. A black plastic partition separated the test and control tanks from the clear plastic Y tube. The bottom of the Y tube was covered with sand. As shown in Table 9, the number of macroscopic organisms placed in the test tank varied with the nature of the test. An effort was made to have approximately the same biomass present irrespective of test species.

Specimens of *Clib. tricolor* and *Pagurus miamensis* from storage tanks were placed individually in the stem of the Y tube. The test animal's position was observed five minutes later, except in cases where the specimen crawled over the cloth partition at the end of each arm before the end of the five minutes. If the specimen was still in the stem at the end of the first period, it was left in the Y tube an additional five minutes. If the crab still did not show a choice, it was removed. The sand in the Y tube was stirred about after each test to eliminate the possibility of "trail"

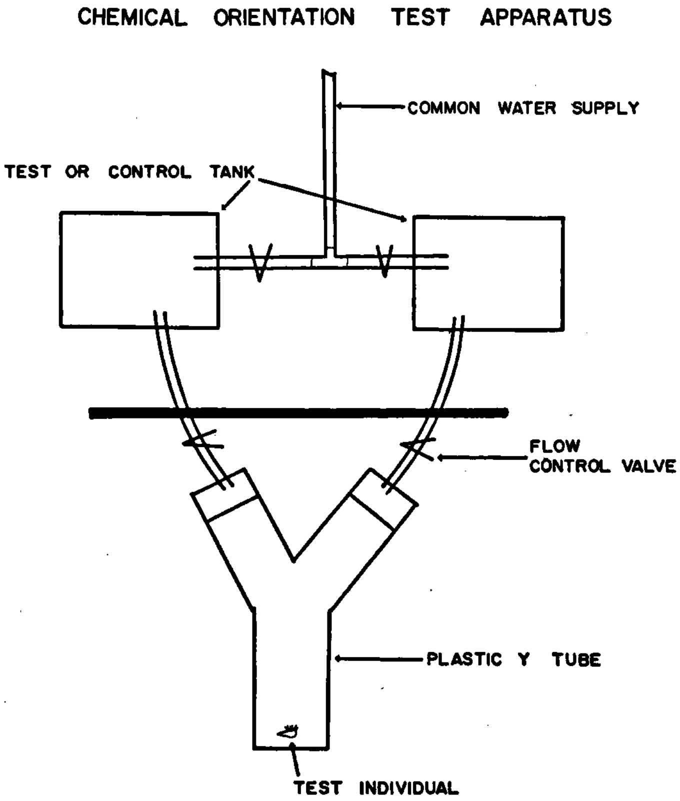


Fig. 37. Diagram of apparatus used in chemical orientation tests.

following. Test replications were separated by at least five minutes. The supply tubes from the test and control tanks were alternated after every ten tests to counteract any position preference of these hermit crabs. The positions of the test and control tanks were also interchanged occasionally. Unless otherwise specified the tests were run during the day, when crabs of the species being tested normally were aggregated in the field. Chi-square tests were calculated on the distribution of choices between test and control arms of the Y tube. The results of these tests are shown in Table 9.

In all cases, the test and control tanks had sand from the same source covering their bottoms.

The results of the experiments, in which individuals of *Clibanarius tricolor* were tested for orientation toward water which came from a tank containing a group of *C. tricolor*, were statistically very significant in both the 1962 and 1963 series. For simplicity, the results are grouped in item #1 of Table 9. The empty mollusc shells used in item #4 had formerly been occupied by specimens of *C. tricolor*. They were emptied, washed for a number of hours in running sea water, washed in 70%

Table 9

Chemical Orientation Tests

Clibanarius tricolor					
#1	Test	100–200 *C. tricolor*		89	chi^2 = 21.4
	Control	empty tank		37	$p < .01$
#2	Test	100 *Cal. tibicen*		28	chi^2 ± 6.4
	Control	empty tank		12	$.02 > p > .01$
#3	Test	100–200 *C. tricolor*		28	chi^2 = 0.0
	Control	100 *Cal. tibicen*		28	$p > .90$
#4	Test	empty mollusc shells		25	chi^2 = 1.1
	Control	empty tank		18	$p > .25$
#5	Test	12 *Uca rapax*		14	chi^2 = 4.2
	Control	empty tank		27	$p < .05$
#6	Test	20 *Mithrax verrucosus*		13	chi^2 = 11.52
	Control	empty tank		37	$p < .01$
#7	Test	detritus rock	daytime	25	chi^2 = 0.02
	Control	empty tank		24	$p > .90$
#8	Test	detritus rock	night	30	chi^2 = 5.80
	Control	empty tank		14	$p < .02$
Pagurus miamensis					
#9	Test	100–150 *P. miamensis*		38	chi^2 = 2.60
	Control	empty tank		17	$p > .10$
#10	Test	detritus rock	daytime	28	chi^2 = 0.02
	Control	empty tank		29	$p > .90$
#11	Test	detritus rock	night	19	chi^2 = 2.08
	Control	empty tank		29	$p > .10$
#12	Test	"home" rock & 90 *P. miam.*		42	chi^2 = 6.20
	Control	empty tank		22	$p < .02$

ethanol twice, and then washed in running sea water for another hour. The small number of fiddler crabs (*Uca rapax*) used (12) were sufficient to fill the test tank. Even with this small number of individuals, the crabs did not appear to adjust to the clear water, sand bottom and/or crowded conditions; they were in a highly distrubed state throughout the testing (limbs grossly extended and rigid, frequent limb autotomy). The specimens had been collected from a mudflat, in turbid water that was left in isolated pools during low tide and was presumably subject to temperature flucuations. Their lack of adjustment to the test apparatus was not as unexpected as was the avoidance shown by individuals of *C. tricolor*. Likewise, the strong avoidance of the water coming from the tank containing spider crabs (*Mithrax verrucosus*) was surprising. It should be noted that although these spider crabs adjusted better to the test apparatus, they were constantly fighting actively and/or going through aggressive displays toward one another. For the tests listed in items #7 and #8, one or two detritus-covered rocks were placed in the test tank. These rocks were of the type upon which *C. tricolor* normally feeds at night. Tests were run in the morning (0600–1200 hrs; item #7), well before aggregations in the field begin their daily emigration and in the late evening and night (18.00–22.00 hrs; item #8), when individuals in the field are spread out over the feeding grounds. The tests of item #8 were the only ones using *C. tricolor* that were carried out during the evening or night. Pilot experiments in 1962 indicated that there is no orientation toward aggregations of *C. tricolor* after about 16.00 hrs. Therefore the tests for chemical orientations were carried out between 06.00–14.00 hrs.

The same time restrictions applied in the tests with *Pagurus miamensis*, except that diurnal testing was always stopped before 12.00 hrs due to the earlier emigration of the groups of this species. The detritus rocks used were taken from the areas of groups formation and feeding. These two areas are less distinct in *P. miamensis* in that the crabs feed on rocks in the same faunal-ecological microzone that they group in. The tests listed in item #12 were carried out using a slightly different procedure. A detritus-covered rock similar to those used in the tests of items #10 and #11 was placed in the test tank. When this rock was taken from the field, it had five individuals of *P. miamensis* on it. These crabs, plus 85 from a storage tank were allowed to settle on the rock in the test tank and this artificial micro-community was undisturbed for over 36 hours before testing was started. Individuals to be tested were taken from the group on the rock. After the first 50 tests, 20 more individuals were placed in the tank and were undisturbed for over 24 hours. Testing was carried out from 05.00 to 10.00 hrs in order to maximize the possibility of detection of any orientation tendency. As is seen from Table 9, it was only under these most favorable conditions that a statistically significant chemical orientation was shown by members of this species.

The results of these orientation experiments indicate the presence of a number of interesting chemically elicited reactions. In the first place, individuals of *Clibanarius tricolor* do orient chemically toward a group of conspecific individuals. This orientation could aid in formation and/or maintenance of the diurnal aggregation. The orientation did not occur at night when the crabs are normally dispersed over the feeding area. However, the orientation was not species-specific, as shown by the reactions given in the tests using groups of *Calcinus tibicen*. When given a choice, individuals of *Clib. tricolor* showed no preference between a conspecific group and a group of *Cal. tibicen*. The tests with empty shells (item #4) indicated that the crab's shell is not important in its chemical orientation toward a group of crabs (no orientation shown, $p > .25$).

The second and rather surprising set of results was the avoidance of both fiddler crabs (whose limbs were rigidly extended, crabs apparently in "shock") and spider crabs (which were continually fighting). These crabs were utilized simply because they were available, representative, nonpagurid crustaceans. I wished to see if positive orientation by *Clibanarius tricolor* was limited to members of the same family. The strong avoidance shown tends to disqualify the results for the above-mentioned purpose, but they are of interest themselves. They suggest the possibility that crabs in "shock" or engaged in a high level of aggressive interactions give off a chemical that other crabs can detect and avoid. Another possible explanation is that some property of the particular species themselves was avoided by individuals of *C. tricolor.*

The third result was the crab's orientation at night, but not during the day, toward a detritus-covered rock (their normal food source). These tests show that chemical cues are important and multiple in the behavior of *Clibanarius tricolor.*

The tests with *Pagurus miamensis* showed that this species does not orient toward a group of conspecific individuals or to the type or rock they aggregate upon in the field. However individuals did orient toward the combination of these two objects. The latter result most nearly approaches natural conditions and thus chemical cues appear to be of importance in this behavior in this species.

TACTILE STIMULI

In 1962 another series of experiments was carried out in the analysis of the cues involved in the aggregation formation of *Clibanarius tricolor.*

A large enamel pan was visually divided into four quadrants by placing small spots on the sides of the pan. The bottom was covered with sand and two sets of items were placed in two of the quadrants. A set of shells from which the individuals of *Clibanarius tricolor* had been removed was placed in one quadrant and a set of small stones of approximately the same size and coloration as the shells placed in another. In the first series of tests, the shells were washed only with sea water. In the second series, the shells were first washed in 70% ethanol and subsequently washed in sea water. The test individuals were placed in the center of the pan and their position noted 5, 10 15, and 20 minutes later. The quadrants of the stones and shells were altered after every five tests. The results are listed in the table below, along with the chisquare values and probabilities for the distribution of positions among the four quadrants (chi^2_1) and of the distribution of positions between the stones and shells (chi^2_2).

	Sea water wash			*Ethanol wash*		
	#	chi^2_1	chi^2_2	#	chi^2_1	chi^2_2
Shells	19	30.20	4.46	45	34.80	1.60
Stones	8	$p < .005$	$p < .05$	34	$p < .005$	$p < .10$
Controls	5			22		

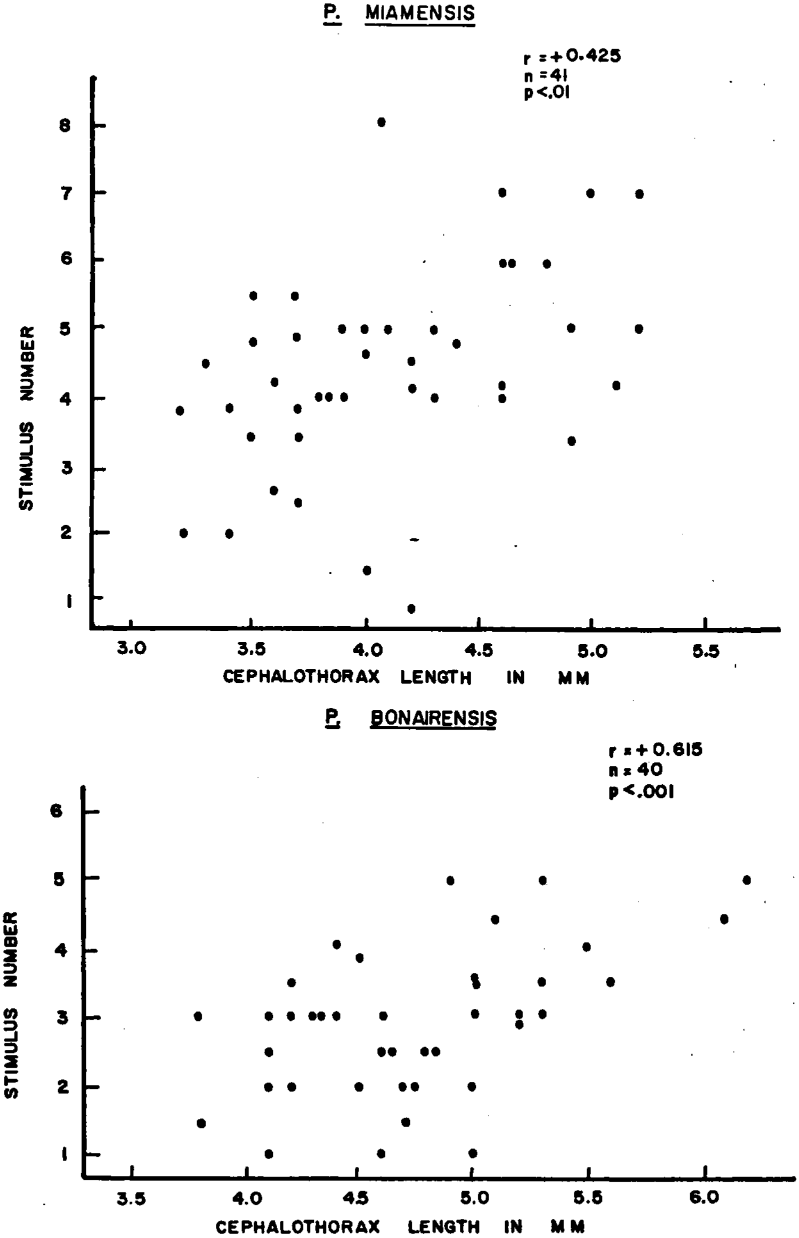


Fig. 38–39. Relationship of size and average weight eliciting dislodging-shaking in *Pagurus miamensis* and *P. bonairensis*.

The results of these tests indicate that the crabs do orient to the shell chemically (or perhaps by chemo-tactile means) and to shells or stones tactilely and/or visually. Apparantly the substance oriented to can be washed off by ethanol.

As described in earlier sections, the individuals of the genera *Pagurus* and *Pylopagurus* show a distinct shaking behavior pattern when another individual crawls upon their backs. This behavior pattern tends to dislodge a crab that is on the back of the shaking individual. Since specimens often went through this dislodging behavior pattern when the individual-to-be-dislodged appeared to be out of their visual range, it seemed that this behavior might be initiated by tactile stimuli. (The possible existence of special chemical or sound cues was not tested.)

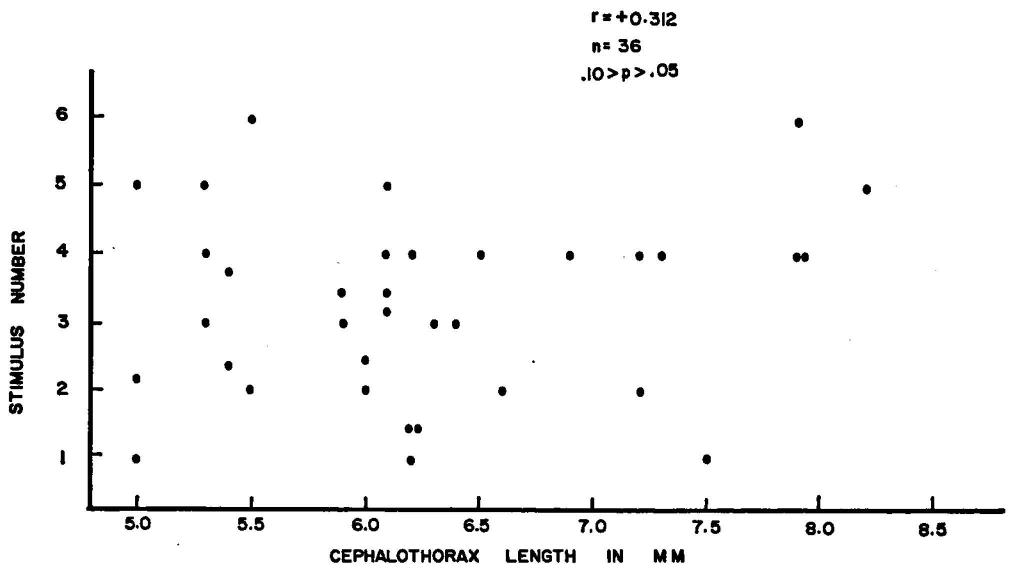
Pilot experiments indicated that individuals would respond to artificial wire "legs" placed onto their backs. A series of artificial legs was fashioned from steel wire, one mm in diameter and about nine cm long. To vary the weight of these "legs", lumps of clay of varying size were attached to the wire.

The legs were weighed on a Reyers and Zoon, type PM balance. The legs were supported in such a way that when balanced, they made an angle of 30° with the balance pans. A series of 50 individuals of each species was tested. The specimen to be tested was placed in a culture dish, eight cm in diameter, with sand on the bottom. The water level in each dish was such that the highest portion of the test crab's shell was just below the water surface. The animal was undisturbed for five minutes. It was then tested with all the weights used for the species (see Table 10). Each test leg was placed on the highest area of the shell of that individual. Approach and placement were from the back of the crab to minimize visual disturbance. The legs were supported in such a way that they made a 30° angle with the crab's substratum. There was an interval of at least one minute between the testing of different weights. The weights whose placement caused dislodging-shaking were recorded.

TABLE 10

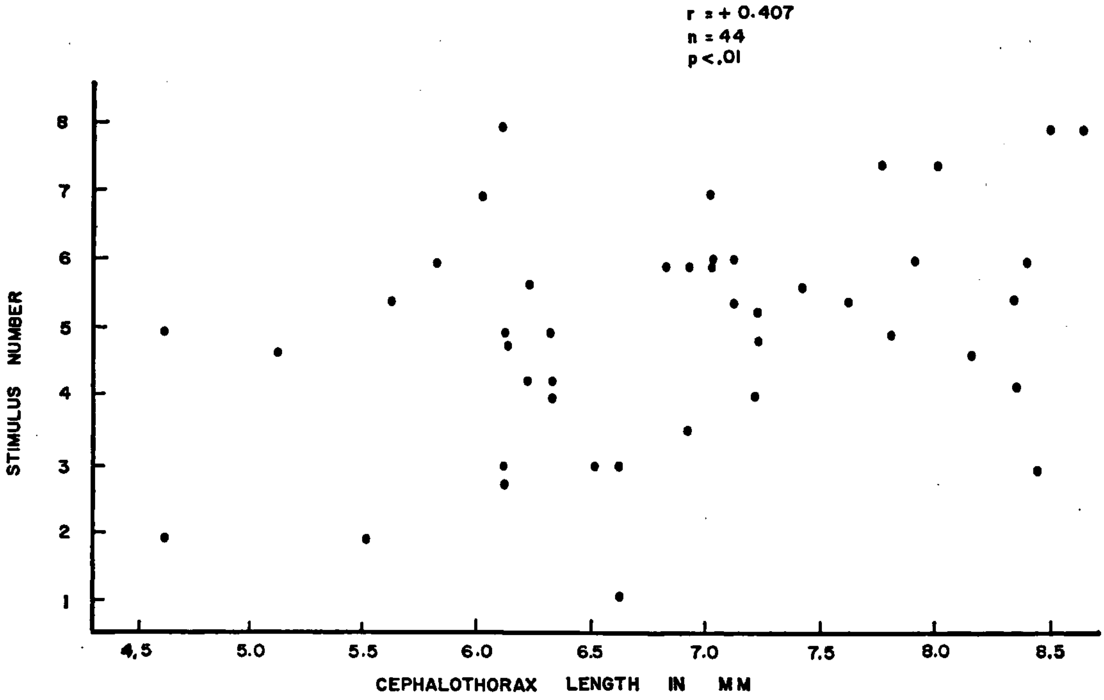
WEIGHTS USED IN ANALYSIS OF DISLODGING-SHAKING STIMULI

mg	40	180	200	280	410	480	585	880	1,255	2,770
Pagurus miamensis	1	2	3	4	5	6	7	8		
Pagurus bonairensis			1	2	3	4	5	6		
Pagurus marshi					1	2	3	4	5	6
Pylopagurus operculatus			1	2	3	4	5	6	7	8



P. MARSHI

r = +0.312
n = 36
.10 > p > .05



PYLO. OPERCULATUS

r = + 0.407
n = 44
p < .01

Following testing, the specimen was weighed in its shell, and then extracted and the length of the cephalothorax measured. Subsequently the average weight responded to by each individual (who responded to any weight) was plotted against its cephalothorax length. A Pearson's r correlation coefficient was determined for the distribution and the probability of such a distribution occurring by chance alone determined from statistical tables.

The response distributions and the statistics for each are given in Figures 38, 39, 40 and 41.

Observations during the testing and initial inspection of the results suggested that the size of the shell an individual was inhabiting affected its responses to the weights. That is, individuals of the same size varied in their behavior according to the weight of the shell they were in. A weight/length index value was obtained for each specimen by dividing the combined animal-shell weight for each specimen in milligrams by the length of the cephalothorax in millimeters. This index failed to correlate more closly than the c.l. values with the average value of the weights thrown off. However, it did show some correlation, in two species, with the number of different weights to which individuals responded (see table below). The negative correllation in *Pagurus bonairensis* and *Pylopagurus operculatus* indicates the tendency of individuals in relatively lighter shells, to react to a greater range of stimuli.

CORRELATION OF W/L INDEX WITH # OF WEIGHTS THROWN OFF

	r	p
Pagurus miamensis	— 0.073	> .10
Pagurus marshi	0.039	> .10
Paguris bonairensis	— 0.240	.10 > .05
Pylopagurus operculatus	— 0.255	.10 > .05

Fig. 40–41. Relationship of size and average weight eliciting dislodging-shaking in *Pagurus marshi* and *Pylopagurus operculatus*.

DISCUSSION

An axiom of animal behavior is that the movements of an organism at any time will, in part, be caused by the physical conditions of and variations in the organism's environment. Its genetic framework and past experience up to that moment will determine how the organism will react in response to a given change in any one or more of these conditions. In my study of these crabs, I ignored or only briefly considered many of the abiotic factors. Also, I left uninvestigated the genetic framework of the animals and the changes in behavior both during maturation and over long periods of their lives. Rather, by observation and experimentation, an attempt was made to investigate those behavior patterns, which are elicited and controlled for the most part by the presence and movements of individuals of the same species.

DISTRIBUTION AND DISPERSION

The first aspect of social behavior encountered in this approach was the statial distribution of the crabs in nature. The species of hermit crabs examined are confined to warm marine waters from the shore-line down to a depth of about 30 meters. Within these broad ecological limits, genera and species are more narrowly confined by various physical aspects of the environment. *Paguristes* species are able to live in deeper waters and, around Curaçao, *Pts. cadenati* is limited to deep-water areas. *Calcinus tibicen* is more tolerant for some variation in depth but is not found in waters as deep as *Pts. cadenati.*

The genera *Pagurus* and *Pylopagurus* are limited to slightly more shallow areas than *Calcinus*, and *Clibanarius* species tend to be even more shallowly distributed. From another viewpoint, *Clibanarius* and *Pagurus bonairensis* are able to inhabit shallow, turbid waters such as in the inner bays of Curaçao. These areas are very rich in organic deposits both on the mudflats per se and in the slightly deeper bay bottoms. This is especially true in comparison with the organically poor marine waters of the Netherlands Antilles. *Clibanarius cubensis* and *C. vittatus* (in Florida) are able to inhabit mudflat areas more readily than *C. tricolor. Clibanarius antillensis* is found in the same mudflat environment but is much smaller and probably feeds on smaller particles. *Pagurus bonairensis* is able to invade even more turbid waters and exploit this detritus-rich niche.

Associated with depth restrictions are the limits imposed on species' distributions by water circulation and oxygenation level. This includes restrictions such as those caused by the extreme wave action along the north coast of Curaçao, which probably contributes to the absence of most species of hermit crabs there. Also, many areas along the south coast have no hermit crabs present, apparently because of local heavy wave action. No doubt the extra weight and the added external surface that the crab's gastropod shell impose help to restrict the distribution of the organisms in these areas.

Another important environmental factor is the presence of food. Hermit crabs in general are omnivorous. All the species studied were readily maintained in the laboratory on a diet of canned dog food. Individuals of all species would attack the macroscopic pieces and tear them apart with one or both chelipeds and further macerate the particles with their maxillipeds and other mouth parts. Large pieces of both brown and green algae were less actively manipulated. Although most species did appear to feed upon macroscopic algae to a limited extent, the level of feeding activity of a group was more readily increased by the introduction of either animal matter or small detritus-covered rocks. In the field, all species appeared to concentrate their feeding activity largely on detritus matter. Experiments described in an earlier section of this paper showed that individuals of *Clibanarius tricolor* orient chemically toward a detritus-covered rock during the species' period of feeding. Macroscopic particles of animal matter were fed upon by hermit crabs as well as other crustaceans; however, in all species the majority of the individuals appear to be feeding on detritus material during the majority of the species' feeding period. In areas where the bottom is either sandy or composed of clean rocks, few or no individuals of any species of hermit crab were found. The density of hermit crabs (all species considered) varied from 0 to 928 individuals per square meter in the areas sampled. The average density of the selected areas measured was 220.5 hermit crabs per square meter.

In addition to the above mentioned factors, the distribution of individuals of a species within any given area may be influenced by the distribution of rocks, corals and other large objects. Positive thigmotaxis and/or negative phototaxis (see DREZEWINA 1907) would provide a behaviorally simple way of congregating individuals under large rocks. Such a type of distribution was observed in *Calcinus tibicen*. Distributions formed in a uniform (laboratory) environment were random. The distribution of *Pagurus marshi* (within favorable areas) was almost random in the field.

Even after considering the limitations set by the variations of ecological and microgeographical conditions, the distribution of individuals of most of the shallow-water hermit crabs studied was not random. Non-random distributions are the rule among animals (WYNNE-EDWARDS 1962) and have been mentioned in a qualitative way for some European species of hermit crabs (BOHN 1902). The degree of contagiousness both in the laboratory and in nature varied from species to species and within species depending upon ecological conditons.

Clibanarius tricolor was the most consistently highly gregarious species, although *Pagurus miamensis* and *P. bonairensis* were also consistently distributed contagiously. Even individuals of those species which were too uncommon or were distributed in places that made measurement difficult (i.e. *Pylopaguris operculatus* and *Pagurus pygmaeus* under rock piles), appeared to be distributed contagiously. In *Clibanarius tricolor, Pagurus miamensis* and *Calcinus tibicen,* groups are formed which appear to be relatively stable from day to day. In *C. tricolor* the individuals form and/or maintain the group guided by chemical orientation to conspecific individuals. *Pagurus miamensis* and *Calcinus tibicen* appear to orient toward factors of the local physical environment when forming their groups. In the shallow waters near a marine shore, it may be advantageous not to depend on the permanence of particular rocks for maintaining group stability. The establishment of a definitive and stable aggregation may be more essential in *C. tricolor,* due to its limitation to shallow water. Groups exposed at low tide retained a small but consistent amount of moisture around the inner members, while isolated individuals usually moved to deeper water during low tide. By aggregating toward one another, groups of *C. tricolor* eliminate dependence on rocks or other larger objects in the environment, which could be displaced. The diurnal aggregations of any species may be of an advantage insofar as predators can more rapidly learn that hermit crabs are protected by their gastropod shells.

Another distributional factor was noted for *Clibanarius tricolor.* Within the large aggregations which this species forms, the large males tended to be on the periphery of the group.

Experiments described in an earlier section showed that several stimuli contribute to the formation and/or maintenance or these aggregations. In the case of *Pagurus miamensis,* the combination of a detritus-covered rock with conspecific individuals upon it acts as a source of chemical substances to which the crabs orient. Individuals of *Clibanarius tricolor* will orient to a chemical coming from a group of *tricolor* (or *Calcinus tibicen*). This "grouping pheromone" is not species specific, but tests with fiddler (*Uca*) and spider crabs (*Mithrax*) indicated that this chemical is not a property of all Crustacea. It would be hard to imagine how a chemical orienting stimulus could work over any distance in the turbulence of a marine shore. Because of the complexity of the movements of the transporting medium, it is assumed that in nature these chemical stimuli are effective in directing orientation, only over relatively short distances. As shown by the work of BOSSERT & WILSON (1963), even traces of pheromones in microgram quantities can effectively excite through thousands of cubic meters of space, but their directive potential is greatly reduced by the turbulence of a medium such as the waters of an ocean shore.

Laboratory tests indicated that the gastropod shell does not act as a source of a distance-orientation chemical but that there may be an ethanol-soluble chemotactic factor present on the shells. *Clibanarius tricolor* did orient preferentially to a pile of empty shells when they had been washed in sea water. However, after the shells had been leached in ethanol, no preference was shown between a pile of shells and a pile of small stones. Even so, the crabs did orient toward both the shells and stones in preference to the control areas, indicating the possible presence of a tactile element in the aggregation formation of *C. tricolor*. Tests concerned with any visual cue in aggregation formation were negative.

DIEL CYCLES

The diel cycle variation in the locomotor and feeding activity of these crabs appeared to conform to one or the other of two general patterns. The more common was a diel cycle in the strict sense, i.e. varying in the same way each day and controlled or guided by the physical changes associated with the 24–hour cycle. This was found in *Paguristes grayi, Pts. cadenati, Pagurus marshi, P. miamensis*, *P. pygmaeus, Calcinus tibicen, Pylopagurus operculatus* and *Clibanarius tricolor*. It is of course possible that the cycles of these species are affected by factors whose variations are of a different period. However, the principle variations are correlated with variations of a daily nature.

The second pattern was the tidal variation that was possible present in *Clibanarius cubensis, C. vittatus* and *Pagurus bonairensis*. An activity pattern based on tidal movements would be logical for these species and field observations indicated that his may be the case. If the crabs are to exploit the rich environment of the mudflats and yet avoid being exposed completely to air during low tide, their activity must be correlated with the rhytm of tidal variation.

Among those species with a diel cylce, several types of patterns appeared. The most common was a nocturnal, crepuscular-peaked pattern. *Clibanarius tricolor, C. antillensis, Calcinus tibicen, Pagurus miamensis, P. pygmaeus* and *Pylopagurus operculatus* move about and feed during the evening and at night and show peaks in their locomotor activity at dawn and dusk as they return to and move out from areas of diurnal aggregation. In all these species, the diurnal group, whether formed through true gregariousness or orientation to local environmental features, is a quiescent aggregation. The organisms move about little and feeding movements occur at a low rate during the day. In late afternoon or evening, the "group" breaks up and the crabs move away several meters, feeding throughout the night. Shortly before sunrise the individuals move back into the areas of diurnal grouping.

The cycle of *Pagurus marshi* differs from the above in that its locomotor activity level is highest around dawn; the level of activity is at a moderate, approximately equal level during the day and night but decreases markedly at dusk. In both species of *Paguristes* studied, the pattern is even more anti-crepuscular with low levels of activity at dawn and dusk. It is reasonable to assume that both predators and competition may have been important in the evolution of the cycles of the three species. *Pagurus marshi* differs from other shallow-water hermits of Curaçao in the "boldness" of its diurnal movements. It moves about on top of rocks and coral rubble much more consistently than other species. The detritus camouflage and the decrease in activity at dusk may allow it to survive while thus exposed.

AGGRESSIVE BEHAVIOR

The specific activities of hermit crabs at any moment are strongly influenced by conspecific individuals. The various actions and reactions of crabs which come into contact with one another have been described about in general and specific cases. The model-presentation experiments described above showed that these movements and positions are visual stimuli. The chemical orientation tests and the tactile stimuli tests carried out with pagurid species showed that stimuli affecting other sensory modalities may affect the specific movements that an individual executes at any given instance. A striking fact discovered in this study is the similarity of the behavior patterns among the species observed. See Table 11 for a qualitative summary of the behavior patterns observed in all species. The closest similarity was observed in the general aggressive interactions. Certain types of movements were observable in all species studied. These classes of movements were also seen in several other species of hermit crabs though these species were not observed enough to merit a detailed treatment; these included *Dardanus venosus* (H. Milne-Edwards) and *Petrochirus diogenes* (Linnaeus) in Curaçao, and *Pagurus longicarpus* Say in Massachusetts.

Variations of the more common aggressive displays occurred in some species. The forward ambulatory movement of *Clibanarius cubensis* and the "sidearm" cheliped extension of *Pylopagurus operculatus* are examples. However, these variations were always less frequent in the aggressive interactions of the species. This rareness makes the establishment of the display function of these behavior patterns more difficult. If we were to use the simple information measure provided by the formula $H = -\sum p_i \log p_i$, where p_i is the probabilty of occurrence of even p (SHANNON & WEAVER 1949), rare events do not greatly increase the amount of information in a system. These rare events, even if very effective in eliciting a change in the behavior of the other animal, would not increase the amount of information in the system very much. However, if effective biologically, these rare events may be very important, thus raising an important qualification in the biological use of this information measure.

The common aggressive displays, the cheliped extension and the ambulatory raise, occur rather frequently in all species (with the possible exception of *Petrochirus diogenes*). The frequency of occurrence varies from species to species but these display are not rare in any. The fact that similar movements occur in all members of a group may have several bases. It is unlikely that these movements have been inherited by all living species from a common ancestor. Perhaps, any organism with the morphology of a hermit crab (therefore classified as such) would execute such movements in an aggressive situation. A third possibility is that the not uncommon event of interspecific meetings has necessitated the development of a common language. Crabs of different species, genera and families do meet, and if they could not communicate on a signal level, such meetings could more frequently lead to physical aggression and damage. However, the size differences between species decrease the use of aggressive displays in interspecific encounters. A smaller crab will usually retreat or pull back into its shell at the approach of a larger crab (whether conspecific or not). Indeed the aggressive displays, in particular the ambulatory raise and the cheliped presentation, make the displaying animal appear larger, and their effectiveness as aggressive signals may be related directly to this property. It may be recalled that in vertebrates, agonistic posturing commonly includes swelling, fluffing of feathers, or raising of crests to increase apparent size.

Whatever the basis(–es) for the similarity of the aggressive displays among hermit crabs, the differences observed in the frequency of occurrence and manner of execution for the most part follow phylogenetic lines. Thus the behavior of *Clibanarius tricolor* and *antillensis* are almost identical, as are the patterns of *C. cubensis* and *vittatus*. However, these two pairs are rather distinct from each other and behaviorally could be put in separate subgenera. The general speed of movement, manner of walking, rigidity of appendage during the execution of an ambulatory raise and details of shell-fighting all separate these pairs. Moreover, the preliminary observations of the sexual behavior of *C. cubensis* & *vittatus* indicated even more definite separation and closer relationships with the genus *Paguristes*. BOHN (1902) has suggested that the genus *Clibanarius* was derived from a *Paguristes*-like ancestor.

The behavior of *Calcinus tibicen* is similar to that of *C. tricolor* & *antillensis*. The similarities are more numerous than those between the two species pairs within the genus *Clibanarius*. However, the unequal and larger chelipeds of *Calcinus tibicen* are used more, and their movements are stronger aggressive stimuli, than the chelipeds of any *Clibanarius* species. PROVENZANO (1959) has mentioned that the differences in cheliped morphology is one of the few areas of difference between the genera. As described in the earler sections of this paper, this similarity between *Clib. tricolor* & *antillensis* and *Cal. tibicen* extends also to the details of their sexual behavior patterns.

The pagurid species studied can be ranked according to the size of their major cheliped, frequency of use and importance of the major cheliped extension display. With reference to the size of the major cheliped, the order is *Pagurus bonairensis*, *miamensis*, *pygmaeus*, *marshi* and *Pylopagurus operculatus*, going from the narrowest to the widest dactyl. Order by frequency of use, the species arrangement would be changed by placing *P. bonairensis* between *P. marshi* and *Pylo. operculatus*. Using the chi-square values of the results of the static model presentations as a measure of importance or effectiveness, the order is the same as the morphologically based one: *P. bonairensis* ($chi^2 = 17.77$), *P. miamensis* (21.19), *P. marshi* (21.30) and *Pylo. operculatus* (24.20). Yet in all these crabs, one or more types of ambulatory movements also occur and are effective aggressive displays. The ambulatory raise of *Pylo. operculatus* occurred quite frequently – 293 times in 1,021 interactions and did act as a stimulus in the model presentation tests ($chi^2 = 11.27$). The similarity of *P. miamensis* and *pygmaeus* is evident in their behavior patterns as well as in their morphology. However they do not appear to be as similar as the species pairs mentioned in the genus *Clibanarius*.

The genus *Pylopagurus* is very paguroid in its behavior. Indeed, among the species studied in Curaçao, *Pylo. operculatus* would appear to be the most strongly different from the diogenid crabs. Dislodging-shaking is very strongly developed, the spasmodic-shaking movements dominate shell-fighting, its general movements are very rapid and the movements of the chelipeds are more frequent and effective in aggressive interactions.

It is possible to speculate upon the development and ritualization (TINBERGEN 1951) of these aggressive displays. The walking movements of all hermit crabs involve some vertical elements. In *Clibanarius tricolor* and *Calcinus tibicen*, these elements are small, while in *Clibanarius cubensis* and *Paguristes cadenati* they are quite noticeable. Moreover, as one crab starts to climb over the shell of another, it raises its ambulatories even more markedly. The fact that the outward motion of the ambulatories makes the animal appear larger is probably important.

Individuals which avoided physical damage by conspecific individuals, by retreating from a larger crab as it walked toward them, would be more likely to survive and reproduce. Likewise, individuals would be selectively superior if the physical damage between crabs was further reduced by the exaggeration, when meeting a conspecific crab, of the vertical element of the ambulatory movements involved in walking or climbing. These improvements in communications would also increase fitness at a population, as well as at an individual level.

In a similar manner, the feeding movements of the chelipeds could have become exaggerated and ritualized as aggressive displays. It is to be expected that more aggressive interactions would occur at a food source than elsewhere. As these crabs feed, their cheliped(s) moves back and forth between the substratum and their mouthparts. The motion need only be exaggerated in its forward component and a cheliped extension would have been executed. It is plausible that the evolution of unequal chelipeds is, in part, a specialization such that crabs can simultaneously display aggressively and feed (with their minor cheliped).

SHELL-FIGHTING

Unlike the general aggressive repertoire, shell-fighting and sexual behavior patterns are strongly divided along familial lines. The general framework of shell-fighting behavior is similar in all species and those factors which were indicated as important for *Clibanarius tricolor* probably are effective in all species. That is, a smaller crab can very rarely get a larger (non-soft) crab out of its gastropod shell; that females may have a slight advantage in shell-fights; and that recently moulted individuals are more subject to attack and more likely to lose a shell-fight.

In addition, observations indicated that in all species, with the possible exception of *Paguristes* species, the application of direct force between crabs does not take place, but rather the behavior patterns which an attacking crab goes through act as signal stimuli. Several persönal communications and the papers of BOUVIER (1892), BOHN (1903) and ALLEE & DOUGLIS (1945) have indicated rather clearly the idea that the evacuation of one crab by another is a matter of force. However, almost without exception, these observations have been of fights between an artificially shell-less crab and one in a shell. Such a situation could exist in nature but all the fights I have observed both in the laboratory and in the field have been between two shell-inhabiting individuals. These observations include two shell-fights between individuals of *Pagurus longicarpus*, the species observed by ALLEE & DOUGLIS (1945). These fights followed the general pagurid pattern and included both rapping and spasmodic shaking.

The actual effective stimuli of a shell-fight which affect the defending crab's peripheral sense organs and eventually its CNS, can only be guessed at. However, behaviorally it is clear that the actions of the attacking crab which result in eviction of the loser are acting at a signal level. The rapping motions of diogenid crabs and the rapping and spasmodic shaking in pagurid crabs are probably negative situations which the defending crab would avoid if possible. Evacuation is one means of avoiding them. The loser of a shell-fight does not appear to be physically damaged in any way.

The first actions of an attacking crab are to either attain an opposed position directly or to turn the other crab over and over while holding the shell in its ambulatories. Both REESE'S (1962a, 1963) and GRANT'S (1963) work on the shell-selecting behavior of hermit crabs have indicated that the weight of a shell is an important factor in selection. It is probable that the attacker is visually and, in the case of a recently moulted defender-to-be, chemically oriented to a shell of approximately the right size. Then through its initial turning and cheliped insertions the crab could measure the shell more closely. These measurements could include "weighing" the shell (and occupant). The positioning behavior which precedes rapping or spasmodic shaking may also allow the crab to "judge" some variable of the shell, as well as orient itself for the behavior patterns to follow.

Preliminary observations of the shell-fighting of *Dardanus venosus* indicated that in this species, the rapping movements follow the pattern set by the positioning movements. That is, the positioning movements involve a side-to-side horizontal figure 8 motion by the attacking crab. In the same way, the rapping is not carried out directly up and down along the midline of the shell aperture, but raps are executed first on one side and then on the other. Often the attacker gave two raps on the left, raised itself and moved to the other side of the aperture and executed two raps. Sometimes when the crab's apertures were directly opposite, a slight downward motion occurred – but just a dip, not a full rap. The raps were generally diogenid in nature of execution.

The fact that the repertoire of pagurid crabs is more complicated than that of diogenid crabs can be interpreted in several ways. Spasmodic shaking may have been present in the "ancestoral" behavior pattern and could have been lost in diogenid crabs. Conversely it may have been added onto the ancestral pattern in the pagurids while the diogenid line evolved no such complications. It could be argued that making noise (rapping) in the deeper waters characteristic of the Paguridae as a whole is undesirable in that it could attract predators while such noise would be undetectable among the surf and snapping shrimp sounds of the shallower areas which are characteristic of the Diogenidae as a whole. The argument would be weakened by the diogenid pattern of *Paguristes* species unless one considers the shortened series of raps and overall reduction in number of raps per fight characteristic of *Pts. cadenati* and *grayi*. Associated with this reduction in these species is the apparent use of some force in pulling the loser out. It may be that this type of behavior is not as advanced, less "signalized" in this genus.

After the shell-fighting behavior patterns are accepted as symbolic stimuli, a possible explanation of their ritualization may be given. If a crab did grasp the limb of another with its cheliped and attempt to pull it out forcefully, it might not be successful on the first pull. A series of tugs by an attacker could be given added force by bringing the large abdominal muscles into play and using a rapid downward motion of the attacker's shell to apply a sudden outward force on the limb(s) grasped by the attacker. However, this strategy could often lead to autotomy of a limb by the defending crab. This would not only damage the defending crab but it would also not obtain the fought-for shell for the attacking crab. The evolution of a signal level strategy such as present in most species would eliminate or greatly reduce physical damage between combatants and at the same time assure the possibility of attainment of the shell by the attacking crab, when it is larger.

SEXUAL BEHAVIOR

The difference between the families in the species' sexual behavior

TABLE 11

SUMMARY OF THE BEHAVIORS OBSERVED AMONG THE PAGURIDAE OF CURAÇAO

	Aggressive Movements						Shell-Fighting		Sexual			
	Ambulatory Raise	Second Ambulatory Display	Cheliped Extension	Cheliped Presentation	Second Cheliped Movement	Dislodging-Shaking	Rapping	Spasmodic Shaking	Rotating	Jerking	Post-copulatory	Normal Moult-copul. Sequence
Clibanarius tricolor	×××	—	×	—	—	—	×××	—	×××	—	×××	×××
Clibanarius antillensis	×××	—	×	—	—	—	×××	—	×××	—	×××	×××
Clibanarius cubensis	×××	×	××	××	—	—	×××	—	××	—		
Clibanarius vittatus	×××	×	××	××	—	—	×××	—				
Calcinus tibicen	×××	—	×××	××	—	—	×××	—	×××	—	×	×××
Paguristes cadenati	×××	×	××	××	—	—	×××	—	××	—	×	×
Paguristes grayi	×××	—	××	×	—	—	×××	—				
Pagurus miamensis	×××	×	×××	×××	—	××	×	××	×	××	×	×××
Pagurus pygmaeus	×××	—	×××	×××	—	××	××	××	×	—	××	×××
Pagurus bonairensis	××	—	×××	×××	—	××	×	××	×	×××	××	—
Pagurus marshi	××	—	×××	×××	—	××	×	××	×	×××	××	×××
Pylopagurus operculatus	×××	×	×××	×××	×	×××	—	×××				

××× = Common ×× = Moderately Common × = Rare — = Absent patterns are also marked and consistent. The differences have been discussed in the species descriptions, in particular, under *Clibanarius tricolor* and *Paguris miamensis*, and are summarized in Table 11. In the Paguridae, the similarity in the motions involved in shell-fighting and sexual behavior is worthy of mention. Although effected by different movements, spasmodic shaking and precopulatory jerking both involve a short, rapid movement of the passive crab toward the active crab. As mentioned above, the sexual behavior of *Clibanarius cubensis* and *vittatus* more closely resembles that of *Paguristes cadenati*, while *Clibanarius tricolor* & *antillensis* and *Calcinus tibicen* show many similarities. The closely related pairs of *C. tricolor* & *antillensis* and *Pagurus miamensis* & *pygmaeus* appear to illustrate a case of ecological vs. sexual isolating mechanisms. That is, in Curaçao, *C. tricolor* and *antillensis* are ecologically separated for the most part, and their mating patterns appear to be very similar, if not the same. *Pagurus miamensis* and *pygmaeus* live in the same microenvironment and their patterns are very different In fact *pygmaeus's* pattern is the most divergent among the pagurid species observed. It would appear that the presence of two closely related species in the same microenvironment has necessitated the development of very different and distinctive patterns of sexual behavior.

It is interesting to speculate on the possible basis for the difference in the physiological-behavioral sequence in the mating behavior of *Pagurus bonairensis*. In the majority of matings in all other species observed, the female released matured larvae, moulted and then copulated. The sequence in *P. bonairensis* appears to be copulation, release and then moulting. The environment of *bonairensis* presents several features that might be disadvantageous for recently released larvae: the water temperature is slightly higher during the day, the oxygenation level is probably rather low, and wave action is so slight that the larvae might easily settle into the mud bottom and die if they do not swim away (not into the shore) on their own. Thus perhaps it is necessary for the female to migrate to slightly deeper waters (of Piscadera Baai) to release the larvae. This would present no problem in the copulation-fertilization sequence unless the male does not migrate, and fertilization of the new eggs occurs in deeper waters after egg release and moult, by the breaking open of the attached spermatophore filaments. In other bay-inhabiting species, such a movement to different ecological conditions would involve a much shorter movement, just off of the mudflats (which have to be vacated at low tide in any event). The slope of the bottom in the area inhabited by *Pagurus bonairensis* is such that a longer migration would be necessary. (Mating behavior in the populations around Miami, where this species is rather widespread, appears to follow the "normal" pattern of release, moult and copulation.)

The more common sequence of mating activity for crustaceans is illustrated by *Clibanarius tricolor*. Shortly before she is ready to moult, a female is contacted by a male and he begins an extended series of precopulatory behavior patterns.

After the female has moulted (with the help of the male in some cases in *C. tricolor*) a series of behavioral acts leads to copulation. In *C. tricolor*, there follows a period of postcopulatory behavior which appears to be similar in movements to the precopulatory activities. This activity may aid and/or protect the female while she is getting the new eggs in place.

SOCIAL DOMINANCE

The observations of laboratory groups over a period of days provided several interesting sets of data. Considering the aggressive behaviors of the whole group, it is clear that the aggressive activity of a group declines rapidly over several days and reaches a low, perhaps constant, level. This was observed in all three species studied (*Clib. tricolor, Cal. tibicen* and *Pag. miamensis*). The amount of aggressive behavior decreased rapidly after initial introduction, placement in a new tank and a second isolation-re-introduction. The lower level of aggressive behavior seen on the days following one of the three treatments is probably more representative of the conditions present in nature. The measurements of the diel activity of the various species indicated that the amount of aggressive activity varies throughout the 24 hours. This cycle is correlated rather well with the variation in general locomotor activity. Variations in aggressive behavior as measured under laboratory conditions, appeared to be present in nature also and are only to be expected if the animals maintain a relatively constant aggressive predisposition.

The interactions of the individuals of a group of animals may occur according to two sets of rules. Operating under the first set, every interaction is decided by the interaction of two "anonymous" organisms. That is, the two organisms are of a certain size, physiological condition and each have a history of social interactions which may effect their future actions in a general way. However the effects of an animal's history are not oriented toward specific individuals but rather produce behavioral predispositions. SEWARD'S (1946) work on submissive behavior in the rat illustrates such predispositions induced by behavioral history. According to the second set of rules, the outcome of any given interaction is mainly determined by the history of interactions of the animals with respect to each other as specific individuals. The organisms recognize one another and the outcome of the interaction is decided largely by the effects of previous encounters. This second set of rules operates in the maintenance of a dominance or "peck" order while the first set plays a more important role in the establishment of the order.

A group of organisms may interact in a stable, ordered fashion and be operating only according to the first set of rules. That is, every interaction is decided strictly on the basis of the interaction of independent operators. Consistent, ordered differences between individuals could however produce a consistent, ordered pattern of interactions.

The groups of crabs set up in the laboratory did show a certain amount of order in their patterns of interactions. The combining of the interactions occurring when the group was first formed, with the results of later interactions may have badly obscured the outcome. However, let us examine the manner in which such data can be treated. If the groups are arranged in a peck-right or absolute straight-line order (as was done in the top matrix of Figures 32, 33 and 34), it is observed that the results of a number of interactions are not consistent with such an arrangement. Even when arranged in a peck-dominance or percentage, straight-line order, there are interactions which do no appear to fit such a pattern. Thus although the interactions of most of the groups were far from randomly arranged (as shown by the D.H.S.) they did not completely fit any of the standard types of dominance orders.

The covering matrix for each group is also of interest. In any sort of social "order" (except an absolute straight-line order), such a matrix would be of the type observed in these crabs. That is, in many of the groups of crabs, almost every individual was chain-dominant over almost every other individual. In an absolute dominance order, the animals would be chain-dominant over 19, 18, 17, 16, etc. organisms from the alpha individual down. This was hardly the case in these groups. The results of the chain-dominance matrices agrees closely in many ways with the subset groupings which were based only upon the first-order interactions. For the most part, subset grouping based on the covering matrices differ little from those presented. What this agreement points to is the probable total scope of the Dominance Hierarchy Statistic. That is, although it is based on the first-order interactions, it probably reflects the order present in the group, even when considering all possible chains of interactions.

However, what the D.H.S. tells us is of limited value if we are interested in true dominance orders. It does definitely prove that the results of the interactions are not arranged at random and that the crabs are definitely ordered in their interactions even though this order is not perfect. The average D.H.S.'s for the groups of the three species are 3.459 for *Pagurus miamensis*, 3.224 for *Clibanarius tricolor* and 2.849 for *Calcinus tibicen.* All are highly significant ($p \leq .01$). That is, if A is dominant over B and B is dominant over C, then there is a good probability that A is dominant over C. However, the mechanism of this dominance is not elucidated by the D.H.S. In order for this arrangement to be a true dominance order, the crabs must be recognizing each other as individuals (with a certain position relative to themselves).

The problem of proving that the crabs are recognizing one another has not yet been solved. Certain readily observable variations in the data point toward such a system. If the system were based on independent events, which would probably be strongly sizedependent, there should be a correlation between the size range of a group and the perfection of its dominance order. That is, if size were very important, the perfection of a dominance order would depend in part upon the size distribution of the group. Rank order correlation coefficients between size range and the D.H.S. for each group were insignificant ($p > .10$): $c = +0.30$ for *Pagurus miamensis*, $c = -0.40$ for *Clibanarius tricolor* and $c = +0.30$ for *Calcinus tibicen*. In argument against within-group recognition are the variation patterns of the percentage of interactions-with-displays shown by each species (Fig. 29, 30 & 31). If individual recognition was playing a part in the interactions of the group, the percentage of interactions-with-displays should have decreased as group order was established. In all three species, this percentage inconsistently varied about an average approximately equal to the percentage on the first day.

The problem of recognition was not considered in PARDI'S (1948) work on dominance order in *Polistes gallicus*. In the rather extensive work on social orders in *Cambarellus*, LOWE (1956) demonstrated several variations that point toward the presence of recognition and true dominance orders. These facts included subordinate animals retreating at less extreme forms of aggression over a period of time and the fact that a crayfish maintained or lost little of its dominant position after loss of a cheliped.

The detection and demonstration of a true dominance order in the interactions of a group is a difficult problem and more than a matrix of interactions is required. The mathematical methods herein presented can establish that a group is ordered to a certain degree, but the basis of this ordering to a certain degree, but the basis of this ordering is not so"easily" measured.

Through this work, a description of the behavior patterns in a series of hermit crabs had been presented. Based upon this descriptive-experimental basis, a more complete study of the communications systems involved is being carried out (HAZLETT & BOSSERT 1965).

SUMMARY

1. The social behavior patterns of twelve species of hermit crabs found in the waters around Curaçao, N.A. are described. All species showed marked similarity in their aggressive displays, the most common of which are movements of the appendages, called here the ambulatory raise and cheliped extension.

2. Model presentation experiments proved that these positions are effective visual stimuli. These tests also showed that the white tips of the ambulatories of *Clibanarius tricolor* are aggressive stimuli.

3. Pagurid crabs showed a dislodging-shaking behavior pattern when crawled upon by other individuals. Experiments were carried out to determine the relationship between stimulus weight and the size of a crab showing this pattern.

4. Measurement of laboratory and field distributions indicated that some species are truly gregarious (*Clibanarius tricolor, Pagurus miamensis, Pagurus bonairensis*), while other species are contagiously distributed due to orientation to certain physical factors in their environment (*Calcinus tibicen*).

5. Laboratory and field tests showed that individuals of *Clibanarius tricolor* form relatively stable groups. The groups are formed and/or maintained through orientation to a "grouping pheromone". These groups are formed daily after the crabs have been dispersed over the nightly feeding area. At night, individuals of *Clibanarius tricolor* oriented chemically toward a detritus-covered rock, their normal food source. Groups of *Pagurus miamensis* also oriented chemically to a group of conspecific individuals established on a rock. Individuals of both species oriented toward a conspecific group only during the day.

6. Diel cycle measurements were carried out for most species. The most common pattern was a nocturnal, crepuscular-peaked

cycle, although *Paguristes* species showed an anti-crepuscular pattern.

7. Individuals of all species fought one another for gastropod shells. With the possible exception of the genus *Paguristes*, the direct application of force did not play a part in these shell-fights. The signals exchanged by an interacting pair were very different in the two families; in the Paguridae, the attacker shakes the defending crab back and forth rapidly by a movement of its ambulatory legs while the diogenid aggressor strikes the defender's shell with his own by means of abdominal muscles. Measurements of shell-fighting pairs of *Clibanarius tricolor* indicated that smaller individuals very rarely win over larger crabs, females have a slight advantage in shell-fights and that recently moulted crabs are both more likely to be attacked and more likely to lose when attacked.

8. The sexual behavior of most species was observed and described. The precopulatory acts of the male are similar within the Families; diogenid males mainly rotate the female around an axis through the plane of her shell aperture, while pagurids jerk the female toward the male by movements of one of their chelipeds which grasps a female ambulatory leg. The normal larval release-moult-copulate sequence was observed in most species, although pairs of *Pagurus bonairensis* consistently copulated while the female still had a complement of well-developed eggs.

9. A preliminary investigation indicated the presence of social order in groups of *Clibanarius tricolor, Calcinus tibicen* and *Pagurus miamensis,* but the basis for this order was uninvestigated.

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