Some Aspects of the Behaviour of the Soldier Crab, *Mictyris longicarpus*

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THE CRAB, *Mictyris longicarpus* Latreille 1806, belongs to the brachyuran family Mictyridae Dana 1856. According to McNeill (1926) the species ranges northward from southern New South Wales and from Perth, Western Australia, to New Caledonia in the east, to Singapore in the north, and to the Bay of Bengal in the west.

In Australia *Mictyris* is known as the "soldier crab." This appellation is appropriate in view of the habits of the genus. Immense numbers of *M. longicarpus* (Figs. 1 and 2) congregate in dense masses and wander over tidal flats in apparent formation. Their activities exert a particular fascination not only because of these huge "armies," but also because soldier crabs walk forward and not sideways, as do most crabs. Several authors have commented on the habit of *Mictyris* of wandering in armies (McNeill, 1926; Lazarus, 1945; Balss, 1955–56; Altevogt, 1957; Schöne, 1961; Stephenson, 1961). However, little is known of the organisation of this behaviour and I decided to study *M. longicarpus* with a view to describing it. Because of the immediate flight and burrowing reactions of soldier crabs to the disturbing influence of observers, the pattern of behaviour to be described has been previously overlooked.

METHODS

Field observations were made from within a pentagonal plywood hide, 3 ft high, in the sides of which uncovered windows, 11 × 6 inches, were cut. A tripod was used for mounting binoculars and a 16-mm movie camera. On each occasion a place was selected prior to the appearance of the crabs, and observations were made from there for the duration of that particular intertidal period. (Transference of the hide to another area of the beach after the appearance of the crabs invariably disturbed them, and was attempted only a few times.) Apart from the displacement activity to be described later, the crabs did not appear to be disturbed by the presence of the hide.

Field observations were made at least twice a month, and frequently as often as six times a month, throughout 1961 and the first half of 1962. Most of the observations were made at Dunwich, Stradbroke Island and at the mouth of the Pine River (Fig. 3). Localities at which additional observations were made are shown in Figure 3 also.

No period of observation at any one locality was of sufficient duration to allow study of any lunar rhythm in soldier crab activity.

HABITAT

Although Lazarus (1945) stated that *Mictyris* is found "where the mixture of silt and sand is fairly coarse and free from matting mangrove roots," it was observed that the crabs burrow in a wide range of substratum types from silty sand to shell grit. However, material collected from the top 2 inches of a typical *M. longicarpus* habitat at Dunwich (Fig. 3) contained 95–98% sand of particle size 1.96–0.05 mm (F. C. Vohra, personal communication). The method of analysis consisted of removal of gravel, calcium carbonate, and organic matter, followed by sieving the coarse fraction and sedimentation of the fine fraction.

Stephenson (1961) has described the habitat of *M. longicarpus* at Dunwich, where the crabs are found in both clean sand and in areas of muddy sand covered with the eel grass, *Zostera capricorni*. The beach at Dunwich is very wide and flat. No *Zostera* grew in the study area at Pine River, and the beach there has extensive drainage channels in some parts and secondary sand bars in others.

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BEHAVIOUR

Numerous environmental factors such as tide, temperature, solar radiation, precipitation, and wind are generally considered to influence the activities of mobile intertidal animals and of shore crabs in particular (Crane, 1958). Soldier crabs are usually active for several hours before and after low water, although they are more active on warm sunny days than in cold overcast conditions. They were observed to be active at night, but their nocturnal behaviour was not studied. In daylight hours, cessation of activity and retreat below the surface were frequently observed in response to apparently unfavourable conditions, such as the onset of rain. Such periods of retreat ranged from a few minutes to the remainder of an intertidal period.

A pattern of activities is followed by undisturbed populations of *M. longicarpus* during the intertidal period. This pattern will be described as a series of phases of activity, each of which merges with the one following but is nevertheless generally well defined. Variations in the sequence and in the duration of each phase occur, and the pattern may be interrupted or terminated by unfavourable environmental conditions.

1. Subterranean Phase

Activities performed below the surface were not studied, but indications of subterranean activity become obvious some time before the crabs make their appearance. On the surface of the previously smooth sand small hummocks appear and increase in dimensions (Fig. 4). These hummocks are always made prior to the crabs' emergence but their formation does not necessarily imply that the crabs will emerge. Hummock building lasts from 10–30 minutes. Just prior to the second phase of activity the summits of the hummocks are broken open (Fig. 5).

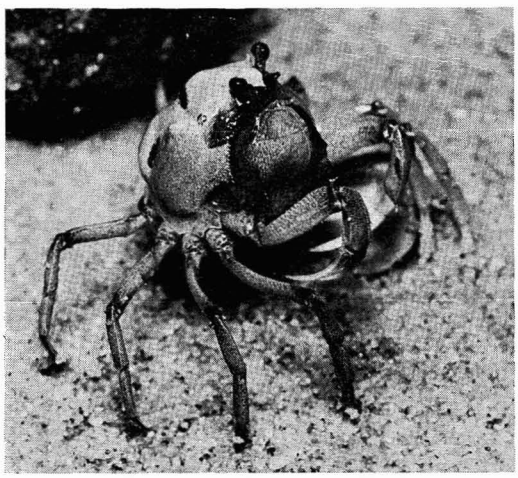

FIG. 1. Adult male *M. longicarpus*. (Photograph by S. Breeden.)

FIG. 2. Section of an army of *M. longicarpus*. (Photograph by B. Morgan.)

2. Emergence Phase

A population may emerge in less than five minutes, or the period may be protracted for as long as one hour. Generally adults emerge before the juveniles. Takahasi's (1935) statement that "*Mictyris* never comes out to the surface" is inexplicable. It was ascertained by digging that many individuals remain beneath the surface for an entire intertidal period. Thus, the emerged population does not represent the total population of the area. Further, the proportion of the population which does emerge varies on subsequent days. At any locality the emerged population may be nearly all adult males on one day, and a mixture of all sizes and both sexes on the following day. McNeill (1926) thought that female *M. longicarpus* do not congregate on the surface to the same extent as do the males. This was verified in the present study.

Upon reaching the surface individuals perform a routine of body care, in which they remove adhering sand grains from the eyes, mouthparts, and carapace. They clean the eye-

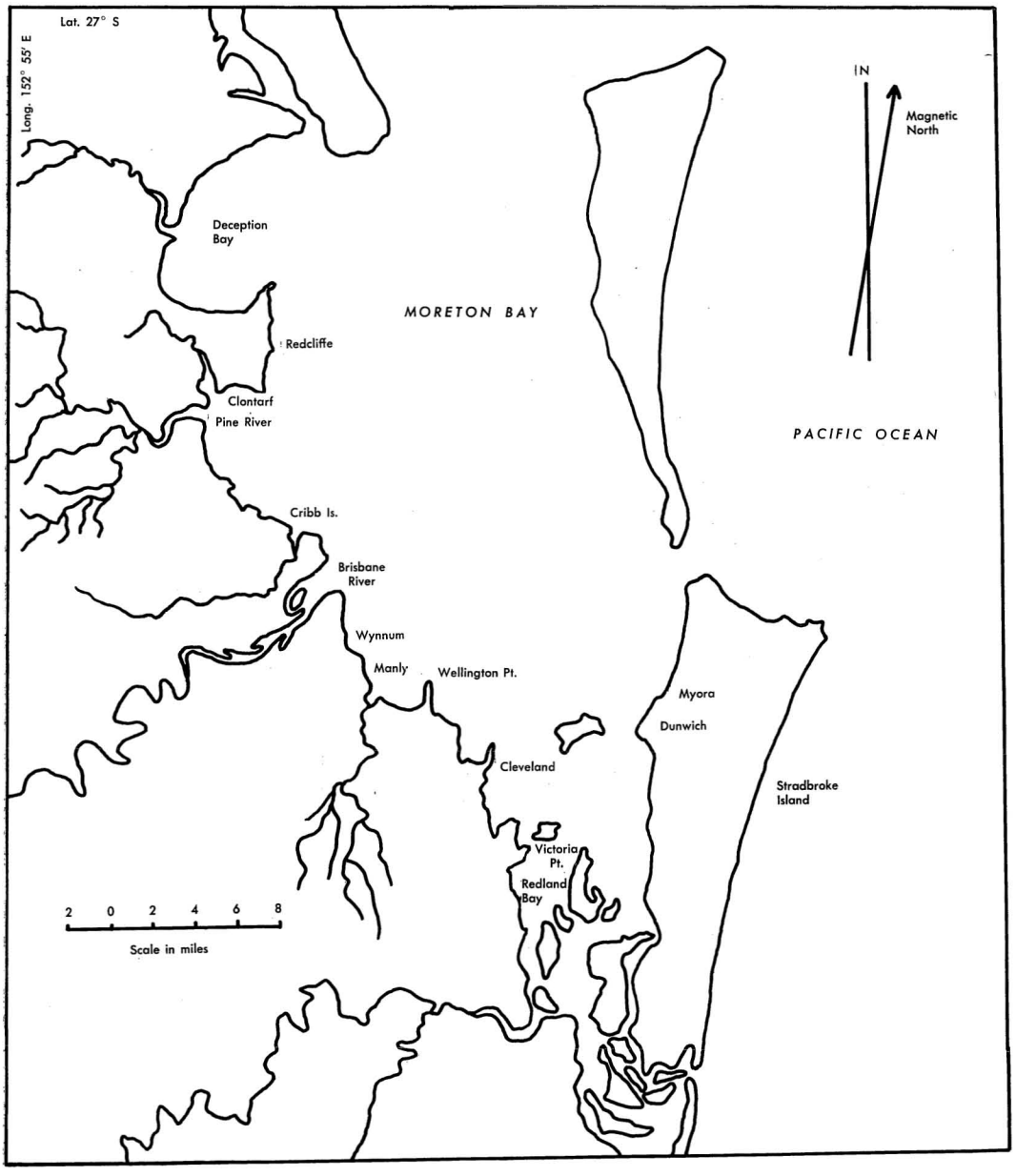

FIG. 3. Map of Moreton Bay, Queensland, showing localities at which field observations were made.

stalks and mouthparts by vigorously rubbing the chelae over these regions. Cleansing is facilitated by vibratory movements of the third maxillipeds and by alternate raising and lowering of the eyestalks. Sand on the carapace is removed as a result of a "back-flip" manoeuvre. This is essentially a half somersault and is executed in less than a second. The crab falls backwards, lies with the carapace on the substratum, and then flips back to the normal resting position.

3. Preliminary Feeding Phase

Subsequent to emergence the crabs feed and walk alternately, the feeding rate being much

slower than that of normal feeding (phase 5). This phase occupies 10–15 minutes. Those crabs which are first to emerge do not immediately feed in this slow fashion, but run about, stop, remain motionless, run further, and so only gradually begin to feed. The slightest disturbance at this stage, such as the flight of a bird overhead, results in their immediate retreat below the surface, from where they emerge again after about 3 minutes.

4. Trekking Phase

Within 15 minutes of emergence the crabs simultaneously begin walking toward the water. This spectacular migration is termed the "trek." Usually the movement is down the beach, but if surface water is present in channels or run-offs the direction of the trek is across the beach toward these channels. Walking of individuals is interrupted by frequent short stops to feed, but the movement of the population as a whole does not stop until the water is reached. Trekking occupies 15 minutes at the most, and is nearly always performed in a virtually straight line from the area of emergence.

There is no cohesion among the individuals during the trek. Each crab makes its own way down the beach and the population appears dispersed at random. Generally, a distance of about 18 inches separates the individuals, which reflects the fact that they have emerged in proximity, and have proceeded at the same rate. Juveniles do not take part in the trek proper. They usually move about 50 yards in the general direction taken by the adults, and then wander about feeding at this level of the beach.

5. Feeding Phase

When they have trekked to areas which apparently are suitably moist, the crabs increase their rate of feeding until it is extremely rapid. They progress as they feed, the direction of movement being more or less along the beach parallel to the water. Frequently, they transverse the *Zostera*-covered areas on beaches where the grass occurs.

McNeill (1926) and Lazarus (1945) have described the mechanics of soldier crab feeding. Portions of the substratum are lifted to the buccal cavity and are sampled by the mouthparts. I observed that material unsuitable for ingestion accumulates at the bases of the third maxillipeds, and is discarded in the form of pellets (Fig. 6) which either drop off, or are wiped away from the ventral surface of the body by a lateral movement of one of the chelae. A similar deposition of discarded material is performed by *Uca* spp. (Miller, 1961) and *Dotilla mictyroides* (Tweedie, 1950). Feeding pellets deposited by crabs in the van are generally left undisturbed by following crabs.

As the feeding phase progresses, the initial rapid rates of walking and of deposition of pellets slow down. Aggregation into groups of about 100 crabs takes place, and the individuals continue to feed, although the groups dissolve and reform continuously. After about ½ hr, the formation of larger aggregations, called armies, takes place. Such groups are distinguished from the former feeding groups in that the individuals of armies tend to remain in company, whereas previously they lacked this cohesion. Feeding continues. The armies increase in size by the addition of recruits either singly or in groups, until aggregations of many hundreds are formed. The duration of the feeding phase is variable. Usually it lasts for about 1 hr, but often can be for as long as 2½ hr. With diminution of the feeding rate, the armies begin to move over the shore, frequently remaining in puddles and run-offs and performing no visible activity.

Examination of the gut contents of soldier crabs was made by dissecting the alimentary canal under the microscope, and staining the organic matter present with Toluidine Blue and Methylene Blue. Almost all the material in the gut was organic debris. Some very fine silt was present, but there were no sand grains in the cardia as reported by Lazarus (1945). Diatoms occurred in all, though not as a major constituent of the contents, and one specimen contained gastropod eggs and a nematode. These data agree with those of Lazarus (1945) who stated that the food of *Mictyris* is "organic fragments and minute organisms" extracted from the sand. However, she remarked that, although "the mouthparts must discard much of this useless sand the gut is usually full of it either in its original state in the cardia or ground into a finer consistency in the intestine." Since soldier

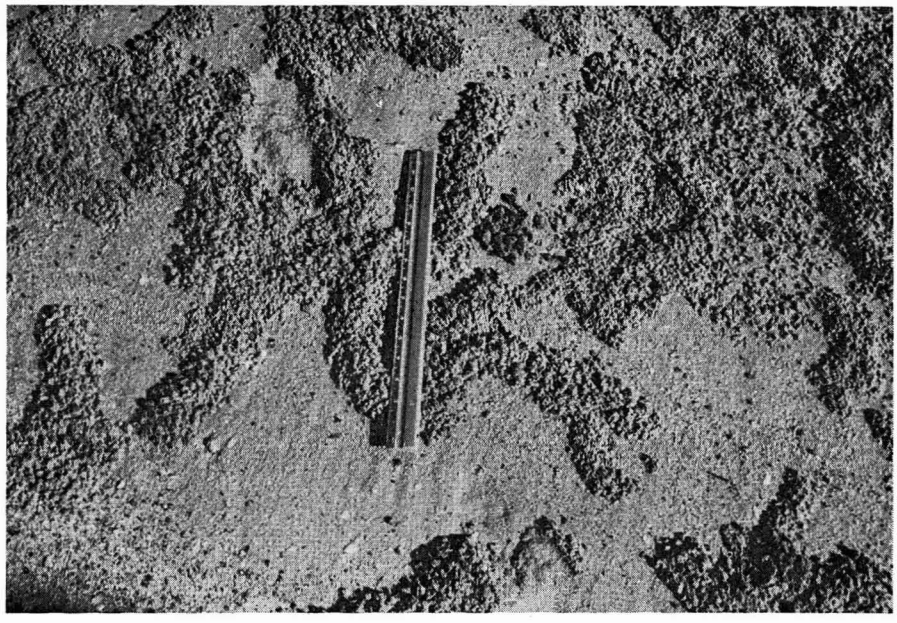

FIG. 4. Hummocks made prior to the emergence of the crabs. (The ruler is 15 inches long.)

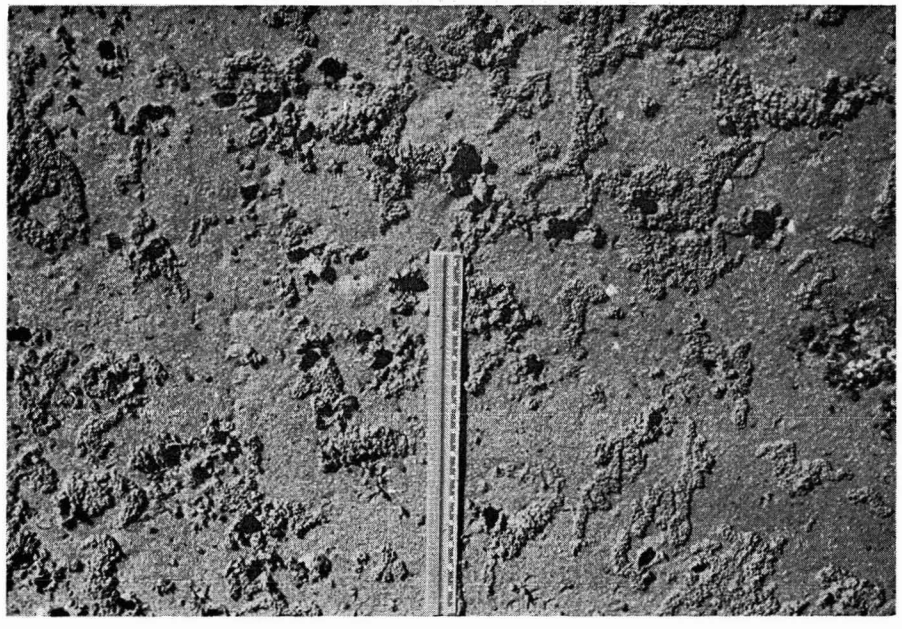

FIG. 5. Holes opened by emergence of the crabs. (The ruler is 15 inches long.)

crabs may feed for periods of the order of 2 hr, it would seem impossible for the gut to accommodate a continuous intake of sand for this length of time. The fact that they habitually feed for such extended periods favours the explanation that they need to sample a large volume of sand, and that they efficiently select from this the small fraction suitable for inges-

tion. Furthermore, the faeces of the animals are devoid of sand grains.

In discussing the feeding mechanism of *Uca,* Miller (1961) remarks that "the thoroughness with which the crabs are able to sort food material from the mineral fraction of the substratum corresponds to the availability of the food material." He showed that the sandy beach-inhabiting *U. pugilator* ingests a minimal amount of sand, whereas for the marsh-inhabiting *U. pugnax* "food is more readily available because the silt with which it is generally associated is of sufficiently fine texture to be ingested." Furthermore, in those ocypodid crabs which possess them, the spoon-tipped setae of the mouthparts are present in greater numbers and exhibit more elaborate spooning in species inhabiting sandy substrata than in species of muddy environments (Crane, 1941, 1943; Altevogt, 1957; Miller, 1961). *Mictyris longicarpus* possesses large numbers of densely packed spooned setae. They are present on the inner surface of the third maxillipeds, the outer and inner surfaces of the second maxillipeds, the basipodite of the first maxillipeds, and the outer surface of the endite of the coxopodite of the first maxillipeds. There are four types of spooned seta, which are shown in Figure 7.

6. Army Wandering Phase

Soldier crab armies present a spectacular sight. They may cover vast areas of the beach and their tightly packed masses create a rustling noise audible at a considerable distance. The army wandering phase begins with the cessation of feeding. Sometimes the transition is sudden but usually it is gradual. Armies are generally composed of similarly sized individuals, usually adult males. Only rarely do females wander in armies, though mixed armies occur. In mixed armies, the largest crabs progress in the vanguard, probably because they walk faster than do the smaller ones. In no sense does any section of an aggregation lead the rest. The advancing front changes continuously, and the crabs often walk over each other, two and three deep, in the general scramble. Crowding may be even worse than this, especially when the advancing front reaches standing water and stops. Armies cover great distances during this phase. They commonly walk as far as 500 yards, the rate of progression being about 10 yards per minute. Army wandering occupies from 30 minutes to 2 hr. When emerged females are present but have not joined armies, their feeding activities

FIG. 6. Feeding pellets deposited by soldier crabs. (The ruler is 15 inches long.)

(phase 5) merge with the return phase (7) described below. Juveniles do not participate in army wandering.

7. Return Phase

The return phase begins when the armies cease to wander about the beach in a seemingly undirected fashion, and orient their progression in the direction of the upper levels of the shore. As they proceed, individuals tend to dissociate themselves from their fellows so that the armies lose their cohesion. The crabs continue walking until they reach the level of the beach at which they emerged. This return may be protracted for as long as 1½ hr, but it may be as short as 15 minutes.

8. Aggressive Wandering Phase

On completion of the return phase, the crabs dig holes in typical corkscrew fashion (McNeill, 1926). Although McNeill believed that these burrowing actions "are probably unique among the Decapoda," Tweedie (1950) has since noted that *Dotilla mictyroides* employs a similar method. Soldier crabs do not remain in these newly dug holes but re-emerge, dig more holes, abandon these in turn, and continue thus for the duration of the phase. At the same time they respond to encounters with one another. Threat displays between pairs of adult males result from these encounters. In each case, one of the pair of crabs involved was temporarily associated with a hole. Females were not observed to participate in such displays. Four types of encounter were observed: (i) walking over an occupied hole, followed by emergence of the occupant and a threat display between him and the intruder; (ii) physical collision of two crabs in the vicinity of a hole, followed by a threat display; (iii) threat display by an occupant at the entrance of a hole, to which another male in the vicinity responded with a threat display; (iv) intrusion by a male into an occupied hole, or digging by a male so close to an occupied hole that its occupant emerged, followed again by a threat display.

Soldier crab threat display is performed as follows: Rival males meet. Each raises the anterior legs off the substratum so that he is balanced on the third and fourth pairs of walking legs, or even on the most posterior pair alone.

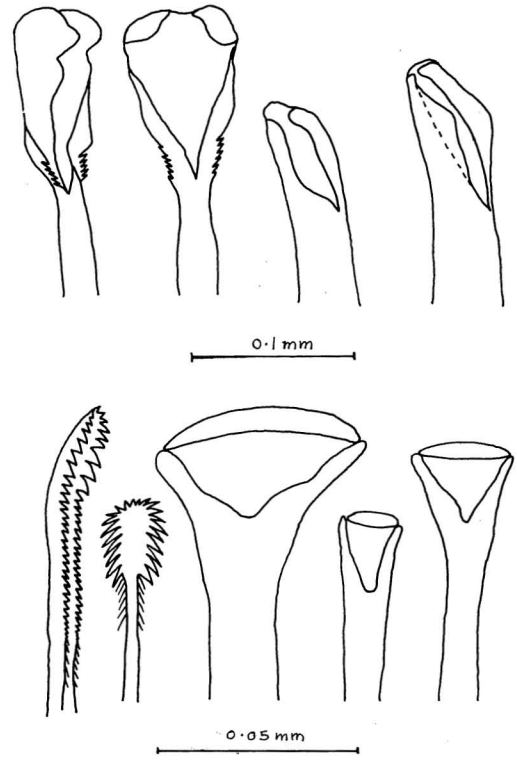

FIG. 7. Camera lucida drawings of the four types of spoon-tipped seta on the mouthparts of *M. longicarpus*.

Those walking legs thus freed are extended laterally, as are the chelipeds. Attainment of the posture of maximum threat occurs when the plane of the thoracic sterna is vertical. Thus, the ventral surfaces of the crabs are brought into proximity. However, they do not touch, and no pushing occurs. The eventual winner may remain poised in the position of maximum threat for up to a second after the loser has fallen away. Throughout the encounter the free walking legs are vibrated rapidly, and the chelipeds are gradually raised vertically from their position of horizontal extension. Immediately after the display the winner exhibits the following characteristics: (i) maximum vertical extension of the chelipeds, (ii) maximum extension of the free walking legs, (iii) maximum extension of the legs on which he is balanced, (iv) maintenance of the eyestalks in the raised position, and (v) maintenance of position with respect to the hole.

The loser is characterized by: (i) lowering of the chelipeds, (ii) flexion of the free walking legs, (iii) flexion of the legs on which he is balanced and subsequent dropping to the substratum, (iv) lowering of the eyestalks, (v) submissive posture in front of the still threatening winner, and (vi) retreat from the vicinity of the hole.

Although the winner may remain in the vicinity of the hole for a few seconds, he generally moves away shortly after the loser has departed.

A stopwatch was used to time 84 threat displays. The longest encounter lasted for 30 sec and the shortest for one sec. From the data collected, the significance of occupancy of a hole, and of disparity in the sizes of the participants were estimated. Occupancy was indicated by a crab's position either within a hole or in its immediate vicinity. Size was subjectively determined with categories of "bigger," "smaller," and "apparently equal." The error in allotting a pair of individuals to the last category may be considerable, but not so great as to obscure the general picture revealed by the data. That this error in categorisation was consistent is indicated by the coefficients of variability calculated for data of threat displays between apparently equal-sized crabs on the one hand, and between unequal-sized crabs on the other. These are 57% and 54%, respectively.

Of 42 threat displays between unequal-sized crabs, 38 were won by the larger of the pair. Less than 10% of these encounters were won by individuals perceptibly smaller than their opponents. Of 40 threat displays between apparently equal-sized crabs, 35 were won by the occupant of the hole. Clearly, occupancy is an advantage.

The mean time of threat displays between apparently equal-sized crabs (9.8 sec) was compared with that of threat displays between unequal-sized crabs (7.8 sec) by use of a "t" test. The means are probably significantly different (p between 0.05 and 0.1), indicating that disparity in size of the participants shortens the time of threat display, compared with that elapsing during threat display between apparently equal-sized crabs.

Only four instances of threat display were observed in which neither participant was in the vicinity of a hole. In each case the larger individual won.

A considerable degree of social facilitation was evident in dense populations of soldier crabs during this aggressive wandering phase. On many occasions threat displays between pairs of crabs were joined by a third, fourth, and even a fifth individual. Each individual participating in these multiple displays assumed the typical threatening posture as far as the crowded space occupied by the several crabs allowed.

Threat display occurred throughout the year. Breeding also occurred throughout the year. In no month from February 1961 to October 1962 were ovigerous females absent in the populations studied.

The aggressive wandering phase may continue for as long as 1½ hr but generally occupies about half that time. Threat displays are frequent throughout the phase. As many as 12 such displays were observed simultaneously in an area 20 ft square. Aggressive wandering diminishes as the individuals remain in holes instead of re-emerging, and the whole population gradually disappears beneath the surface.

For each of these phases of activity during the intertidal period, the approximate duration has been given. It is emphasised that these times are highly variable, and that the entire sequence is not always completed. Although the initiation of each phase is generally synchronised for all the individuals of the emerged population, occasions were noted when feeding, army wandering, and returning were being performed simultaneously in different areas of a large beach.

REACTIONS TO OTHER ORGANISMS

During this study seven species were observed to prey on *M. longicarpus*. They are *Threskiornis spinicollis* (Jameson), the straw-necked ibis; *Halcyon sordidus* (Gould), the mangrove kingfisher; *Egretta alba* (Linné), the white crane; *Sphaeroides hamiltoni* (Richardson), the toad fish; *Ocypode ceratophthalmus* (Pallas), the ghost crab; *Metopograpsus messor* (Forskål), a grapsid crab; and *Conuber sordida* Swainson, a sand snail. The ghost crab and the sand snail preyed on juvenile soldier

crabs. Toad fish captured adults in run-off channels. *M. messor* seized soldier crabs near a rocky point at Dunwich (W. Stephenson, personal communication). The three birds preyed on adults, usually during the army wandering phase of activity. It is noteworthy that, except for a slight increase in the walking rate of the crabs at the approach of a predator, they exhibited no escape reactions. This contrasts strongly with the behaviour of soldier crabs in the presence of human observers. Their reactions in such circumstances are as follows:

1. Burrowing. On being chased by humans, soldier crabs burrow in typical corkscrew fashion.

2. "Fright reflex." *M. longicarpus* occasionally reacts to the presence of an observer by assuming a "frozen" posture in which the limbs are extended rigidly. The presence of normal predators was never observed to elicit this response, common among brachyurans (Schöne, 1961: 474.)

3. Crouching. A crab in this posture lowers the body to the substratum and folds the flexed legs as closely as possible to the body. The eyestalks are lowered.

4. Interspecific threat. Occasionally, crabs which were being chased by the observer, raised the chelipeds and ran away from the observer. This ambivalent behaviour is apparently an attempt to flee and to perform a threat display simultaneously.

5. Displacement feeding. Displacement feeding differs from the autochthonous activity in that any material that is raised to the vicinity of the buccal opening is never introduced into it, and consequently no feeding pellets are formed. Two types of displacement feeding occur.

a. A crab remains stationary, continuously raising and lowering the chelae which may or may not touch the substratum. No material is picked up, and the chelae are not lifted as high vertically as they are in normal feeding.

b. Displacement feeding of the second type has a much more "nervous" appearance (in the sense in which this term is used by Gordon, 1955). Walking with unusually rapid steps, a crab lowers the chelae and picks up material from the substratum in such quantity and with such lack of normal manipulative dexterity as to drop it immediately. The chelae continue their upward movement but do not reach the buccal opening. Furthermore, material not conveyed to the mouthparts during normal feeding is picked up in this displacement feeding, for example, small pebbles and pieces of *Zostera* two inches long.

It is evident that these two types of displacement feeding are essentially similar, differing in their degree of disorientation to the environment, rather than in their organisation. Such correlation between intensity of thwarting or conflict and the degree of disorientation of displacement activity is well documented (Armstrong, 1950).

Circumstances eliciting displacement feeding in *M. longicarpus* are:

(i) Simultaneous activation of the drives to retreat and to stay. Crabs were disturbed by the observer until they retreated, after which the observer remained motionless at a distance of approximately 10 ft. After a few seconds the crabs halted and, while either standing stationary or approaching the position of the observer, began displacement feeding. As they approached, the rate of movement of the chelae increased.

When the observer's hide was placed in such a position that the crabs trekked around or past it, they began displacement feeding as they approached to within about 4 ft. Some individuals spent as long as 3 minutes at a distance of less than 4 ft from the hide, displacement-feeding throughout that interval. Then they made their way past the hide and ceased displacement feeding at about 4 ft from it.

(ii) Simultaneous activation and thwarting of the escape drive. Soldier crabs were chased until they burrowed. When the excavation was as deep as the body of the crab, the crab was removed from it and placed on the surface beside it. The crab burrowed again, and was again interrupted. After about five repetitions of this interruption, some of the crabs so treated began displacement feeding. Many could not be induced to do so, but assumed the crouching posture described above.

All the instances of displacement activity described above were induced by the presence of the observer or of the hide, or by interference.

No displacement activity was observed in any other circumstances.

DISCUSSION

Several aspects of the behaviour of *M. longicarpus* are of interest. It would appear that the preliminary feeding phase may be regarded as appetitive feeding. Normal feeding does not take place until completion of the trek. The obvious result of trekking is that the crabs move from the upper levels of the beach to the more moist areas. Altevogt (1957) postulated that all ocypodid crabs possessing spooned setae on the mouthparts select nutritive material from the sand by the "flotation" method he observed in *Uca* spp. Water is lost continuously through ingestion, evaporation, and in the discarded pellets. Miller (1961) investigated this topic for several species of *Uca* and concluded that the need for water is reflected by the moist condition of the material from which these crabs prefer to feed. This appears to be the case for *M. longicarpus*. Not only do soldier crabs possesses dense spoon-tipped setae, but also they frequently feed in depressions and in run-off channels.

Trekking is most obvious on wide, gently sloping beaches where the crabs may remain on the surface for as long as 4½ hr. Where the beach is narrower and of steeper slope, they do not remain on the surface for such lengths of time, and they generally emerge earlier with respect to the time of low water than do those inhabiting the wider flats. On beaches of unusual configuration, such as those at the mouth of the Pine River, the direction of the trek is determined by the proximity of extensive drainage channels. Moving down the beach would bring them to the elevated sand bars. From the bars to the river the beach slopes in the normal way, and the crabs in this area trek down in the usual fashion.

When feeding has ceased, the army wandering phase takes place. In some respects, the behaviour of soldier crabs in this phase resembles that of *Uca* in the "nonaggressive wandering phase" described by Crane (1958). While it is evident that the aggregations in which feeding takes place subserve coverage of a widely dispersed food supply, the presence of the animals on the surface after feeding has ceased is enigmatic. Whatever are the physiological functions performed at this stage, they must be of considerable significance in view of the energy expended in wandering about the beach, and of the danger from predators to which the aggregations are exposed. These phenomenal aggregations, in which the individuals perform no visible activity other than walking, may be an example of epideictic display (Wynne-Edwards, 1962).

Threat display is associated with competition for space, the space being a hole occupied by one crab and intruded into by another. Occupancy of a hole, however temporary, appears to be the manifestation of a poorly developed territoriality, and for this reason the threat display must be considered reproductive fighting. Tinbergen (1952) remarked that displacement activities occur most frequently during boundary disputes. No instance was observed of either of the participants in a threat display subsequently performing displacement activity. This is not unexpected, in view of the transitory nature of soldier crab "territory," which is based on occupancy of a hole and not on construction and maintenance of a permanent burrow.

There are similarities between the intertidal behaviour patterns of *M. longicarpus* and *Uca* spp. (Crane, 1958). The activities of both are organised into a series of phases. There is a temporal separation of feeding, and of other activities. Although there is nothing comparable with the waving display of *Uca* in the behaviour of *M. longicarpus,* the occurrence in the latter of threat display, and its nature, are of interest.

SUMMARY

1. *Mictyris longicarpus* performs a sequence of phases of activity during the intertidal period: subterranean activity, emergence, preliminary feeding, trekking down the beach, feeding, army wandering, return up the beach, aggressive wandering, return to subterranean burrows.

2. Dense, elaborate spoon-tipped setae are present on the mouthparts of *M. longicarpus*.

3. Wandering in armies occurs after feeding has ceased. Adult males comprise the majority

of these aggregations.

4. Threat display occurs between pairs of adult males. Occupancy of a hole, and larger size of a male, are advantageous in such displays.

5. Displacement feeding occurs as a result of conflict of drives, and of thwarting of a drive.

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