Notes on the Behaviour of Two Estuarine Crab Species

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Summary

(1) The two estuarine crabs, *Helice crassa* and *Hemiplax hirtipes*, at least temporarily, live singly in burrows which they defend from the intrusion of other members of their colonies

(2) Fighting in both species consists mainly of threat display or "ritual"

(3) Exaggerated ritual fighting during peak sexual periods does not seem to function primarily as territory defence

(4) Neither species shows any courtship displays

(5) Both species have efficient means for escaping or concealing themselves from predators

Introduction

Observations of the biology of the crabs *Helice crassa* (Dana) (family Grapsidae) and *Hemiplax hirtipes* (Heller) (family Ocypodidae) were carried out during September, 1954, and from February to August, 1955—i.e., throughout a late summer, autumn, winter, spring Most of the work was done on the mudflats around the Otago Peninsula, but the two crabs are common in similar localities throughout New Zealand

The two species occupy roughly similar habitats estuarine mud flats where they are confined between the tide marks and live in burrows or under stones *Hemiplax hirtipes* is also occasionally found on sheltered rocky shores The two crabs are similar in appearance.

Helice crassa is a smallish crab, about three-quarters of an inch in width across the carapace, olive-green to tawny-brown in colour with rather square proportions when seen from above

In *Hemiplax hirtipes* the carapace is roughly an inch in width and its colour varies from pale blue-green, with a few very small spots, to tawny-brown or reddish-brown with either large masses of purple spots, a pattern of coalesced spots or large purple-blue patches The legs are yellow-green or blue-green and the chelipeds deeper or lighter red on the dorsal edge, white on the ventral edge. The general proportions are rectangular with the long axis extended laterally.

Both crabs typically feed by extracting the organic matter from surface mud or sand, which is picked up indiscriminately by the chelipeds and sorted by the mouth parts They also eat large pieces of dead organic matter, the bodies of dead lugworms, pieces of ascidians, etc.

Crabs of both species can be found occupying burrows *Helice crassa* individuals were observed constructing burrows in the field and in the laboratory. The technique used by these crabs is similar to that described by Dembowski (1926) for the fiddler crab and Cowles (1908) for *Ocypoda arenaria* On no occasion did I see *Hemiplax hirtipes* constructing a burrow, and I suspect that the crabs of this species occupy burrows built by the other.

In a vertical transect of mud bank, *Hemiplax hirtipes* burrows are concentrated near the lower tide limit and *Helice crassa* burrows near the upper tide limit, although there may be considerable overlap between the two distributions. *Helice crassa* is active, feeding and burrowing, mainly when exposed at low tide; *Hemiplax*

hirtipes is active when covered by water during the rising or falling tide Their respective distribution concentrations, therefore, coincide with their feeding and other habits, allowing *Helice crassa* maximum time of exposure and *Hemiplax hirtipes* maximum time of coverage.

Both species live in quite densely populated colonies; the occupation ground is riddled with burrow openings For *Helice crassa* there may be as many as 30 burrows in a square yard of ground surface It is more difficult to estimate numbers of *Hemiplax hirtipes* since they do not correspond one to a burrow as *Helice crassa* tends to; and the *Hemiplax hirtipes* colonies are not as homogeneous However, counts of visible *Hemiplax hirtipes* individuals in a thickly populated colony indicate a density at least as high as that for *Helice crassa.*

Territory

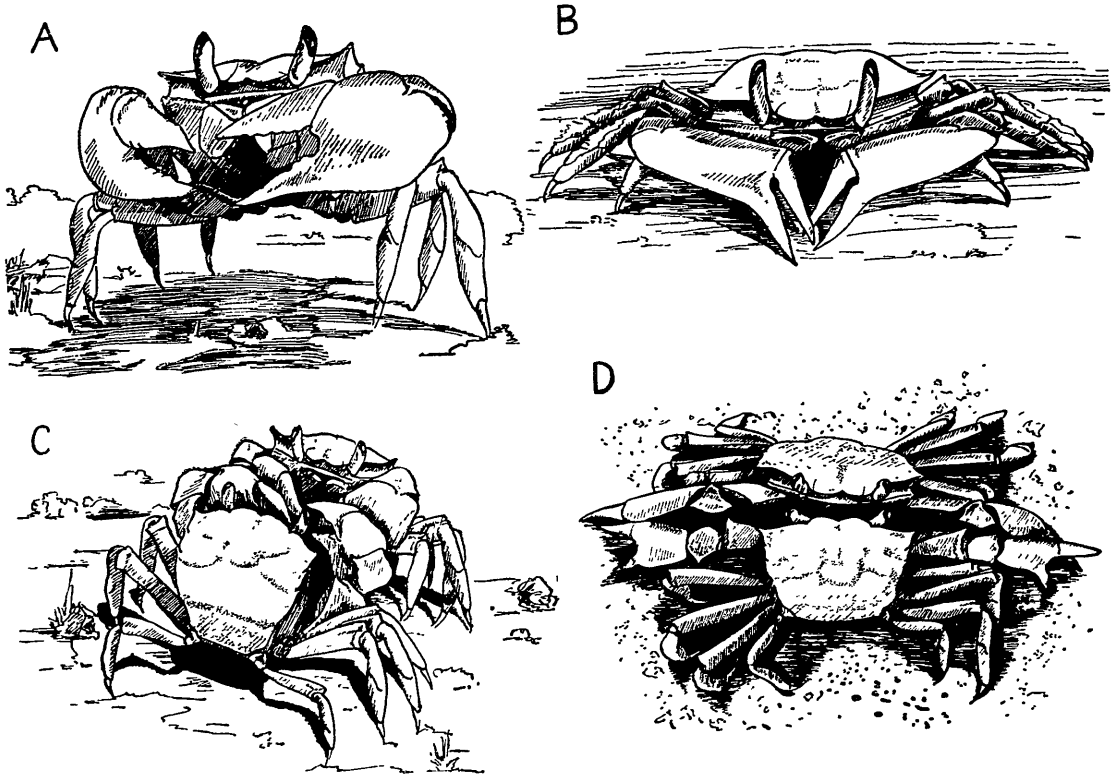
Although these animals congregate in such numbers, there is a minimum of social co-operation between them. Each individual cuts himself off by securing a burrow and defending it and a small area of ground around it from the intrusion of his fellows. At least in *Helice crassa,* this ensures the availability of a shelter for the crab in times of danger, and feeding space as well

To determine the degree to which the animals' activities are localised around their burrows, a set of crabs from both species were differentially marked with fingernail polish on the carapace and leg joints, and close observations and records of their behaviour were kept over a number of days I found that *Hemiplax hirtipes* individuals have a much looser connection with a specific burrow than do individuals of the other species *Helice crassa* seldom moves more than 24 inches from its burrow *Hemiplax hirtipes,* when feeding, wanders over comparatively large areas utilizing and defending not one burrow but any that happens to be at hand.

Fighting

Both crabs defend their temporary or permanent possession of a burrow against other individuals When a wandering crab draws near another's burrow, the occupier of the hole rushes out, or if feeding outside, runs to take up a position at the burrow entrance This may be enough to frighten away the intruder but, if it continues to advance, the defending crab adopts a characteristic "threat" attitude. Bethe (1895) describes this in *Carcinus maenas* as the "Aufbaumreflex". In both species the threat attitude presents to an animal standing in front of the crab the most obvious and—one cannot resist the temptation to say—frightening aspect of its form The chelipeds are raised and held with the "fingers" open and reveal a colour pattern which accentuates their definition and size At the same time the animal spreads or extends its legs to add further to the impression of size (Text-fig 1, Figs. A and B) The adoption of this posture by the defending crab may be enough to send the rival crab scuttling away, but frequently the rival also adopts a threat attitude The two crabs face each other and draw together until their chelae touch *Helice crassa* individuals extend their legs so that the body is raised as high as possible, and raise and flex their chelipeds so that the large pincers are held a little out from the body with their external surfaces directed towards and abutting against those of the rival (Text-fig 1, Fig C)

Hemiplax hirtipes individuals at first hold their chelae open but flexed in such a way as to reveal to best advantage their startling distribution of white and red As they move closer together the combatants extend their chelipeds outwards to the maximum extent Thus they meet with the inside surfaces of their chelipeds turned toward and abutting against those of their opponent (Text-fig 1, Fig D) *Hemiplax hirtipes* does not rise on "tip-toe" but spreads its legs sideways as far as possible bringing the ventral surface of the body close to the ground and emphasizing the impression of width.



TEXT-FIG 1.—Fig A—*Helice crassa,* the threat or "Aufbaumreflex" attitude Fig. B—*Hemiplax hirtipes,* the threat or 'Aufbaumreflex" attitude Fig. C—*Helice crassa,* ritualised fighting. Fig D—*Hemiplax hirtipes,* ritualised fighting

In this position the mouthparts of the two animals are brought quite close together. It seemed from the *Helice crassa* fights observed on the open ground, that its breathing water is often "blown" or "bubbled" into the opponent's face. Probably the breathing currents of *Hemiplax hirtipes*, clinching below the water level, also oppose one another. Opposition of breathing currents may play a part in this ritualised fighting.

Several *Hemiplax hirtipes* individuals timed in this "mutual threat" held it for over five minutes. *Helice crassa* individuals tended to take less time to decide the issue, and this is not surprising since these crabs, exposed on the open ground, are more vulnerable to predator attack. Such fights usually terminate in the retreat of one of the combatants with occasionally the dominant crab pursuing his opponent for a short distance. One contest observed between *Hemiplax hirtipes* individuals lasted an hour and ten minutes and consisted of a series of mutual threatenings and pursuits in which the same crab was dominant throughout. With *Helice crassa* individuals, which are more tied to their burrows, the chance of success in a fight seems to be an inverse function of the distance from the burrow mouth.

In both crabs real fights, involving beating and tearing with pincers, are reduced to a minimum. A whole crab is more likely to survive to breed than an injured one, so that reduction of real fighting has survival value for the species. Real fights were observed between *Helice crassa* individuals on occasions when the intimidation phase tended to be lengthened. One *Helice crassa* male was seen to seize another by a pincer, lift it bodily in the air, and thrust it onto the ground on its back. In other contests limbs were lost or thrown off. Physical struggles seemed to be inevitable when several *Helice crassa* individuals were put together in a laboratory aquarium with little room for escape, and many such crabs were killed or lost all their limbs. Crane (1941) makes the following observation on *Uca*. "Several instances have been observed where crabs with badly damaged chelae, or with chelipeds missing, were definitely bullied by other crabs." In *Helice crassa* under similar circumstances, sick or weak individuals seemed to be the first to succumb.

It appears that *Helice crassa* individuals, male and female, behave in the same way defending a burrow against an intruder of either sex. The males seemed to be readier to fight than the females.

With *Hemiplax hirtipes* fights were observed to take place only between males. No female was observed in the "Aufbaum" attitude. A strange point about defence of property in *Hemiplax hirtipes* is that often a crab which has vigorously and victoriously defended a burrow may almost immediately wander away from it and apparently never return.

At times fighting takes on a rather different character. On May 23 and 24, 1955, both fine clear days, the following field notes were taken:

"8.15 a.m. *Hemiplax hirtipes* males engaged in fighting. Apparently no territorial boundaries are recognized, crabs entering a whole succession of burrows and following each other into the same burrow.

"9.31 a.m. Five crabs contesting the possession of one hole. One crab chases another into the burrow and, after much rushing to and fro with flourishings and measuring of pincers, the defending crab is chased deep into the burrow and forced to vacate by bursting through the roof of a side tunnel. The evicted tenant, after one unsuccessful attempt to regain his property, departs. Three smaller crabs now advance on the burrow and systematically worry the new owner. While two of the new intruders attract the large crab's attention at the tunnel mouth, the third crab enters by the side hole made when the original occupant escaped. The new tenant is forced to defend his prize by rushing backwards and forwards from one opening to the other and brandishing his chelae." I watched this epic struggle for thirty minutes and it was still in progress when I left.

Pearse (1914) states that crabs frequently "dart about without a serious purpose and are sometimes downright mischievous". This description seems to fit similar observations of *Hemiplax hirtipes*

Activities of a similar nature were observed in *Helice crassa.* As with *Hemiplax hirtipes* the warmest and sunniest days provided the most examples, and peak periods of fighting and burrowing seemed to coincide with peak mating periods. During these times some *Helice crassa* males wander far from their burrows and may engage in a series of fights with other wandering males or make raids on other burrows, even going so far as to dig the end-plug out of blocked-up burrows to provoke the owner into defending his territory.

Not only is this fighting without the obvious purpose of more usual territorial defence, it tends to be longer drawn out and more ritualised—i.e., real blows follow threat to a lesser extent.

Most fights, whether on a territory or not, are punctuated by short pauses in which the crabs may perform feeding movements, but in such a rapid and agitated manner that very little mud or sand is conveyed to the mouthparts and no rejection pellets formed Gordon (1955) described such movements in corresponding circumstances for *Uca* species and labelled them "displacement activities"—i e, irrelevant movements performed as a result of a conflict of two drives, the tendency to attack the rival and the tendency to flee from him.

SEXUAL BEHAVIOUR

Mating in *Helice crassa* and *Hemiplax hirtipes* was observed to take place from August to May inclusive, with peak periods of sexual activity in October and May Copulation occurs on the surface of the ground and was observed many times in the field and twice in the laboratory.

Both species exhibit sexual dimorphism with the pincers of the males being much larger than those of the females Crane (1941) reviewed the literature on sexual dimorphism in crabs and concluded that in some crabs the exaggerated pincers of the male are used in courtship display while in other species their function is solely the enhancing of threat against rivals In *Helice crassa* and *Hemiplax hirtipes* no courtship behaviour was observed Nothing like the waving and signalling of the tropical fiddlers described by Crane (1941) was observed Without preliminary overtures the male seizes the female with his pincers and adjusts her body forcibly to the position for copulation as figured by Pearse (1914) for *Uca signatus* Sometimes the female struggles and escapes, but if the male is strong and vigorous enough she becomes submissive

Agitated feeding movements similar to those in the fighting situation were sometimes performed by males attempting to copulate with resisting females These are also reported by Gordon (1955) who again labels them "displacement feeding", but this time resulting from the thwarting of an activated drive

SELF-PRESERVATION MEASURES

Both species are exposed when feeding and present likely prey for kingfishers, herons, gulls, fish and octopods *Hemiplax hirtipes* was also seen to fall victim to a large crab *Hemigrapsus sexdentatus* Awareness of movement is essential for their self-preservation

Helice crassa reacts to any unusual movement within 20 or 30 feet by retreating into the burrow, the restricted area of the feeding range and speed of retreat usually being adequate to keep this species out of trouble. At the first sign of disturbance *Helice crassa* individuals stop feeding and stand motionless Such an alert can be communicated to a large number of feeding crabs, the majority of which do not detect the source of the disturbance If the disturbing element continues to approach, the crabs all scuttle for their burrow entrances Again, individuals

may react to the take-cover movements of other members of the colony instead of directly to the source of the disturbance. As a rule females seem more timid than males The nice discrimination between disturbances and responses must be an asset in the economy of this crab—allowing more time on the open ground for feeding.

In times of danger a frightened *Helice crassa* individual will scuttle into the nearest available burrow whether occupied or not. On one occasion, when sufficient time had elapsed for the crabs to get over their fright, I saw four individuals emerge from the same burrow mouth

Hemiplax hirtipes, which moves to a large extent amongst submerged vegetation and is not as nakedly exposed as *Helice crassa,* can be approached much closer and with much less caution before it runs for cover If, however, their burrows are too far away, *Hemiplax hirtipes* individuals will either try to conceal themselves by burying on the spot or show fight. The burying technique is effective only in soft mud or sand below the water level. The crab first pushes its body backwards into the sand then, with alternate flexure and extension of the posterior legs, covers itself with sand so that its location can be identified only by the agitation of sand particles where the two exhalent breathing currents emerge Crabs kept submerged on sand in the laboratory spent a large part of their time buried in this way

If the animal chooses to show fight, it first adopts the "Aufbaumreflex" attitude but if the source of the disturbance draws closer, the crab stretches itself upwards or sideways to its fullest extent, extends its chelipeds with the pincers wide open. and seizes some part of the intruder This display is mostly bluff, as such crabs cannot inflict much damage on any of their enemies and, if escape is still possible they usually discard the engaged limb and make off at top speed

Adaptive Colouration

Hingston's concept of "colour conflict" (1933) can be applied to the colouration and form of the two crabs According to this theory most animals combine a need for concealment in some situations with a need for conspicuousness in others One solution to the problem is for the animal to have the generally exposed parts of the body cryptically coloured and conspicuous patterns on parts of the body that are revealed by a special posture

When *Helice crassa* is crouched close to the ground and partly buried, all the appendages are folded close to the body and the crab assumes as small and as flat a form as possible The eye-stalks are shut into their grooves in the front of the carapace, and the pincers are folded under the mouth parts, which are pressed toward the ground The back of *Helice crassa* and portions of the appendages still exposed are coloured crytic muddy green, blue green or raw sienna and are difficult to distinguish from the sand on which the animal lies But when the same crab adopts the "Aufbaumreflex" attitude, the ventral surface of the animal is exposed with every part unfolded and extended and the crab looks as big and obvious as possible The pincers, which are the most obvious and wicked-looking feature, are light yellow in colour and edged along the top with sharply contrasting darker green The mouth parts are also light yellow with darker edges Small patches of bright orange pigment are present at the joints of the chelipeds and walking legs visible from the front The light colour and jagged form of the opened pincers make them stand out from the general darker shades of the rest of the animal, and the orange patches are very obvious With the eye-stalks also raised to their full height, there can be no doubt about the conspicuousness of both the animal and its intentions

Hemiplax hirtipes adopts a similar concealing attitude to that of *Helice crassa* with all obvious parts tucked out of sight, the body shape being reduced to as small and compact a mass as possible with only the dark green upper body colouring exposed Often, however, the sand is lighter in colour than the crab and, unless it

can bury itself, the crab can still be seen. *Hemiplax hirtipes* usually shows warning behaviour first and tries to retreat or bury itself only if this fails. As a consequence it is more brightly coloured in the warning fashion than it is camouflaged for concealment When disturbed, this crab turns in the direction of the disturbance and stiffens on outstretched legs with mouth parts lifted from the ground and with the pincers flexed and obvious. Moreover, the crab moves as the source of disturbance moves so that the startling pattern of the pincers is always on display. In this species the pincers carry a band of red and a band of white pigment which contrast sharply with the darker greens and browns of the body and the colour of the sand or mud which may be deepened by the crab's shadow. Closer approach brings about a striking and startling change of attitude, the colourful chelipeds being rapidly extended and the large pincers opened If such intimidation fails the crab finally tries to run away and bury itself

It is possible that the initial warning reaction of *Hemiplax hirtipes* and its fairly conspicuous general colouration are real warning signs of unpleasant taste properties in the crab (proaposematic colouration) For, whereas on numerous occasions predators were seen catching and devouring individuals of *Helice crassa,* on only one occasion was a predator (in this case the crab *Hemigrapsus sexdentatus*) seen to catch and eat an individual *Hemiplax hirtipes*

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