

again at 200 yards south in Region C, where U. marionis individuals sometimes come into contact with U. urvillet individuals, no interspecific aggressiveness was noticed, probably because the individuals of both species are approximately of the same size, so that neither species is able to bully the other.

Under laboratory conditions, where the species were housed in tanks or containers, some unaturally excessive hostile behaviour was noticed at all times of the day. Since each species was housed in a separate container, only intraspecific hostility was observed, and the individuals showing the most aggressiveness were the U. inversa males. For the most part, the individuals of each of the species were confined to tanks too small for their number, so that there was often not sufficient room for every crab to have an adequate burrow. Most of the hostility centred naturally around the ownership of burrows. Moreover, the individuals kept clambering on top of one another in a vain attempt to escape from the tank by climbing up the vertical sides of the container, and this led to further aggravation, and hence to more hostility amongst the crabs. While protecting their burrows, the crabs showed no definite threat-display, as was noticed in the field, but here and there a pair of male individuals could be seen coming to grips with one another for a few moments at a time. For the most part, the more aggressive crabs tended to bully the timid individuals by charging at them in order to chase them away, and, possibly, by actively taking possession of their burrows. For example, a huge male U. inversa individual was seen to walk up to a burrow already occupied by another, somewhat smaller, male crab, whose claw was just visible at the entrance to the burrow. The intruding male attempted to enter the burrow

in spite of its being occupied, but he soon re-emerged, and the rightful owner emerged after him. The intruder lunged sideways at the owner of the burrow who scampered away, and the new male immediately took possession of the burrow.

In the laboratory, too, female individuals, especially those of *U. inervata*, were bullied incessantly by their male counterparts. The only species in which the females appeared nearly to hold their own against the males, was *U. chlorophthalmus*. Because of the unnatural, overcrowded conditions, the females of each species were rather "irritable" amongst themselves. Time and time again, male crabs were seen to charge at females, and they were constantly clambering over them or standing on top of them, in an attempt to escape from the tank.

On the whole, the female *Uca* crab appears to be far less aggressive than the male because, possessing no major cheliped, she is not really able to fight and is relatively unprotected. Although, in the field, she may be warned or chased off the territory of a male crab, she is virtually never attacked by him, probably because she hurries away from him immediately and is adept at scurrying hastily into her burrow, out of harm's way. Her escape is made easier by the fact that she is not hindered by a heavy major cheliped, and so she is able to scamper away from a male very quickly. Moreover, the burrow of the female has a smaller diameter than that of the male, again due to the fact that the female lacks a large cheliped and hence is less bulky than the male. Therefore, once a female has managed to make her escape by running into her burrow, a male crab is unable to follow her down because of his major cheliped. It is obvious then, that, certainly as far as fighting is concerned, the absence of a major cheliped is as important to a female *Uca* crab as its presence is to a male. In their tanks in the laboratory,

however, female crabs were bullied unmercifully by the males, due to the fact that they were apparently unable to make their escape. Because of the overcrowded conditions to which they were subjected, many of the females did not have proper burrows, and the males were quite capable of pushing those who had out of their burrows either to take possession of the latter, or to continue bullying the females still further.

(5) COURTSHIP.

Observations were made on the mating-behaviour of all five *Inhaca* species of *Uca*, and it was found that their breeding-seasons do not quite coincide with each other, some of the species starting to court earlier than others. *U. annulipes*. During July 1954, incipient courtship was beginning to manifest itself amongst the males of this species. Whenever a female approached such a male, he would start to display, beckoning several times with his major cheliped. The display-movement of the major cheliped is precisely the same as that used by the individual when he is threatening any intruders off his territory, a movement which has already been described under "Fighting". When a male is trying to attract the attention of a female, the display-movement used is generally faster, more definite and of a somewhat higher intensity than that observed during threat-display. Such a courting male may jerk from side to side in between his individual beckoning-movements, and he may even run about to a much greater extent than during threat-display. While engaged in threat-display also, the crab jerks about, but to a lesser degree than in courtship, and he tends to remain more or less in one spot while waving his claw and always stays in the near vicinity of his burrow. On the whole, then, the jerking movements from side to side are generally associated with the attracting of a female's attention during courtship, and not so much with threat. Now and then, a

courting male was seen to circle round a female, displaying and feeding at intervals, while the female either scampered off, usually disappearing down her burrow, or continued to feed quite unconcernedly. A certain amount of rivalry over females was exhibited by the males of this species, and this rivalry occasionally led to minor fights between "suitors." On the whole, however, interest in the opposite sex was only starting to be noticeable during the first week of July, and courtship-behaviour was still playing a minor rôle in the lives of the male crabs. A male would frequently appear to lose concentration while courting a female and would resume feeding quite normally. Generally speaking, too, he would appear to forget the female to whom he was displaying as soon as she had entered her burrow, especially if she stayed there for any length of time. There was a noticeable lack of tension in this early courtship behaviour, and the attention of the male easily strayed so that he would display to more than one female within a relatively short period of time. Incipient courtship of *U. annulipes* was particularly noticeable in the open area towards the northern end of Region V of the Saco Swamp. Between 10 and 11 a.m. on one day in particular, when the tide was receding rapidly, such courtship behaviour was noticed amongst those crabs feeding on the drier mud, farthest away from the water. As the day became hotter towards mid-day, this courtship behaviour became more and more evident, but it seemed to slacken off at a steady rate after about 2 p.m., when the day was becoming cooler. Dissection of female *U. annulipes* individuals showed them to have very undeveloped ovaries, correlated with the fact that the mating-period was only in its incipient stages. Females collected during February 1955, were found to have very well-developed ovaries, containing ova which varied in size. During this month, too, very small young *U. annulipes*

individuals were found. In April - May 1955, females collected were found to have undeveloped ovaries without any ova, and again during these months, young individuals were found. Although a certain limited amount of courtship-behaviour, in the form of claw-beckoning to females by male crabs, was noticed again in February and in April - May 1955, unfortunately no observations were made during the actual mating-season which lies between August and January.

U. chlorophthalmus. Also in July 1954, although starting a few days later than in the previous species, incipient courtship was noticed amongst male individuals of this species, but to a somewhat lesser extent than in U. annulipes. As has already been suggested, in U. chlorophthalmus the display-movements are more jerky and are not as clearly defined as those of U. annulipes, whether the individual is courting a female or threatening another male. Again in this species, it was observed that the display-movements were more pronounced and repeated more often when a male was starting to court a female than when he was threatening another male, although the movement was essentially similar in the two cases. During July, the incipient courtship shown by males of this species was noticed towards mid-day at the Saco Swamp, on one side of the pathway towards the northern end of Region B, near the area where the courtship of U. annulipes was particularly observed. Although this early courtship in U. chlorophthalmus began a few days later than in U. annulipes, their display appeared to be of a more intense nature. When a male was beginning to court a particular female, he would stand on or near his burrow, beckoning often with his major cheliped in an attempt to attract the attention of a female. Often he would chase her to her burrow, displaying all the while,

but would soon resume normal feeding once she had disappeared. During the hottest part of the day, two males whose behaviour was typical of this species were kept under constant observation. These two males stood, each for about half-an-hour, at the raised entrance to their burrows, quite motionless. The hot sun dried their carapaces steadily as they stood, each with his large major cheliped held aloft, until the females to whom they were displaying, emerged momentarily from their burrows. The female having thus appeared, the male concerned jerked his major cheliped, the while walking slowly round the raised, characteristically heavy-rimmed, entrance to his burrow. After the female had re-entered her burrow, the male continued to stand motionless as before. Although, particularly during February 1955, one or two *U. annulipes* male individuals were also seen to adopt such statuesque poses with claws raised high, while standing at the entrance to their burrows, this habit was never as noticeable as in *U. chlorophthalmus*. As was noticed in *U. annulipes*, the courting behaviour of *U. chlorophthalmus* seemed to slacken off from about 2 p.m. onwards every day. Again in this species, a certain amount of clay-backoning was observed during February and April - May 1955, but here again the individuals were never under observation during the main breeding-season. Dissected females from July, February and April - May collections were found to have ovaries similar to those of the *U. annulipes* females for the three months, respectively. Like *U. annulipes* too, very small young individuals were found during both February and April - May. *U. inversa*. In this species, the only signs of courtship behaviour in the field were observed during April and May, when certain male and female individuals were seen standing for long periods quite motionless at the entrance to their burrows. In the case of the *U. inversa* males at the burrow-mouths, the major cheliped is not held high but in the normal position of

rest. As in the previous two species, such an individual was not even so much as feeding but simply standing, generally slantwise, at the entrance to his burrow. *U. inversa* is unusual in that the display-movement of the male seems to be used purely as a threat to other individuals and not as a part of courtship behaviour. The nearest approach to what might have been a male courtship display-movement was observed only in certain *U. inversa* individuals kept in captivity during February. For instance, one of these particular male crabs was seen to walk towards a female, which scampered away for a short distance. The male chased after her, and she began to run again but suddenly stopped and stood motionless in one spot. The male individual stopped as suddenly and at almost the same instant as the female, and they stood about two inches apart, more or less facing one another. While holding his major cheliped in its normal position of rest, he began to move his minor cheliped outwards and in again in a more or less regular series of movements, which lasted for some time. Finally, the female ran into her burrow, and the male concerned appeared to lose interest for he soon resumed his feeding. Female *U. inversa* individuals, collected in February, were found to have ovaries which varied somewhat in their degree of development from one individual to another. Although it was never actually observed, it is assumed that mating must have taken place from December to February since young forms of this species were collected during April and May.

U. urvillei. Especially during February 1955, a small population of *U. urvillei* individuals were observed at about 200 yards south in Region C of the Saco Swamp, feeding quietly and lethargically, near their burrows. Nevertheless, these individuals, the majority of which were males, were showing an amount of courting behaviour unusual for the species, and

the male crabs had a special nuptial dress, their carapaces being very shiny and coloured a rich shade of royal-blue. Here and there, an individual's carapace appeared to dry out, and, after disappearing into his or her burrow for a few seconds, the individual would re-emerge, with a shiny carapace once again, and resume feeding. The display-movement of the male crab is precisely the same as that used in threat-display, and hence has already been described in connection with "Fighting". This movement was, however, more frequently seen associated with courtship than with threat, for *U. urvillei* is not very pugnacious. It is of interest to note that neither male nor female individuals stood on raised ground during courtship behaviour. Male crabs were sometimes seen displaying to a female and then more or less chasing her to her burrow. The females, generally speaking, would run rapidly into their burrows at the mere approach of a male crab and would not re-emerge for some time. Very occasionally, however, a male was seen attempting partially to mount a female at the entrance to her burrow, usually for only seconds at a time, since such a female was, as a rule, very timid and would soon hurry into her burrow. Nevertheless, at least four or five partial mounts were observed, each of which lasted for about three minutes. During such a partial mount, which should be the preliminary stage to a copulation, the female generally faced towards her burrow, with the male almost always facing the same way and standing more or less on top of her. From time to time, the male gently stroked the ambulatories and carapace of the female with his major cheliped and ambulatories, and a few of the ambulatories of the female were often seen momentarily to leave the ground. Often, too, with his minor cheliped,

the male would even stroke the eye-stalks of the female until they were temporarily pushed into their orbital grooves. After about three minutes, the female would disappear into her burrow before copulation could take place, and the male would run off, trembling slightly all over his body. Such a female individual was nearly always stroked by more than one male, and a male would court more than one female within a comparatively short period of time. One particular female, which was a great deal less timid than the rest, was partially mounted at the entrance to her burrow by three different males, in quick succession. One or two females, which had been courted quite considerably, were seen to finish their feeding and enter their burrows, which they even plugged behind them. In April - May, the breeding-season of *U. urvillei* was definitely over but, at 200 yards south in Region C of the Saco Swamp, a few males were still in their special nuptial dress. The crabs were feeding as apathetically as before and were showing very little courtship behaviour. No attempts at actual mating were observed.

U. urvillei females collected during February were found to be ovigerous and to have extensive ovaries with large ova. The presence of eggs in the brood-pouch of these females made it quite impossible for copulation to take place and, since most of these eggs appeared to be in a late stage of development, it was evident that the breeding-season was nearing its close. April - May and July females were found to have very undeveloped ovaries.

U. marionis. This species is unique, in that it is the only one with a special breeding-ground, to which the mating individuals move during the breeding-season. The only *U. marionis* breeding-ground observed was situated 200 yards south in Region C of the Saco Swamp, next to the normal feeding-ground of this species, but in the drier more landward,

area nearer the trees. The area was closely observed both during February and April-May 1955, when the individuals were showing marked courtship behaviour and fighting, but very little feeding, particularly towards the middle of the day, when it is hottest. In February, most of the males, like those of *U. urvillei*, had donned a special nuptial dress, which is bright yellow in this species. The males not in nuptial colours were definitely younger, smaller forms, which were darker-coloured. During April-May, at the end of the breeding-season of this species, only one or two such males were still in nuptial dress. Not only during February, however, but also in April-May, the crabs gave the impression of being in a state of high nervous tension, and they were extremely active, spending relatively little time down their burrows, and both sexes were moving relatively long distances from their burrows.

As was noticed for *U. urvillei*, the male courtship display of *U. marionis* involves the same movements as are used during threat-display and have therefore already been described under "fighting", although such display-movements are more commonly seen associated with courtship than with threat. When a male is displaying to a particular female, he usually stands a few inches from the female, generally facing her. Occasionally, however, he may turn his back to her, while dancing more or less round her, a habit which is known as "Revolution", and which Crane (1941) found in only one of her species, *U. beebei*. Now and then, when a male was particularly strongly stimulated by the approach of a female, he would move his major cheliped in an "agitated" manner, which was more typical of *U.* crabs. That is, he would not merely move his major cheliped away from himself, raising it slightly before dropping it, which is the usual display-movement of this species. Rather, he would raise

his bent major cheliped with the claw itself open or closed, at the same time straightening his bent ambulatories until he was standing on their very tips. One or two of the ambulatories would sometimes be lifted momentarily from the ground, and the minor cheliped would usually be lifted slightly. Next, the crab would straighten the major cheliped until it was held out sideways, but pointing high above the body. Finally, the crab would bend the major cheliped in towards himself again, and the normal bent position would again be restored. The minor cheliped would at the same time be dropped, and the ambulatories bent until the normal relaxed stance of the crab was once more adopted. After a brief pause, the movement would be repeated. A female would often seem to respond to the claw-beckoning of a particular male by leading him towards her burrow. This rather wild, stiff, jerky, beckoning-movement of the male was never seen associated with threat-behaviour.

Particularly during February, many female individuals appeared to have scooped up mud either from inside their burrows, or from the ground surrounding them, and to have built small rims round the mouth of their burrows or, at least, little mounds to one side of the mouth, and on these the crabs would stand for long periods at a time. These rims appeared to be of a temporary nature but were nevertheless reminiscent of the heavily rimmed burrows of *U. chlorophthalmus*. Male *U. marionis* individuals did not appear to build rims round their burrows, but, here and there, an individual could be seen reinforcing the entrance to his burrow by "carting" a lump of black mud towards it and, with his minor cheliped and ambulatories, plastering the mud around the mouth of the burrow. It was never established whether or not this habit was associated with courtship, but, since most of the courting males were thus engaged, and the burrows themselves did not

appear to be in any need of repair, it is possible that it was part of the courtship-pattern. From time to time, both male and female individuals appeared to adopt statuesque poses at the mouth of their burrows. The body of such a female would generally slope in towards the burrow-entrance, with one set of ambulatories actually resting in the mouth of the burrow. The rim of the burrow would support the ventral part of the crab's body, and the ambulatories on the side away from the burrow-mouth were generally raised slightly from the ground. The chelipeds and other body-parts were held in their normal positions, with the ambulatories bent. Such a female usually had quite a dry carapace, because she would stand thus for long periods in the sun, quite motionless and not even feeding, possibly waiting for a male to approach her. After a time, such a female would generally re-enter her burrow for a few minutes and then re-emerge, with her carapace wet and shiny again, to resume her normal activities. During April-May only, a few females were observed in a pose somewhat different to the rest. Although they were standing slantwise at the entrance to their burrows like the others, their chelipeds were straightened rather than bent, and their two ambulatories were raised and were sometimes moving very slightly outwards and in again in a rather indefinite display-movement. The ambulatories of such a *U. marionis* female were moved slightly up and down, while the crab remained more or less on the same spot. Here and there, too, a few females were seen to be showing a more definite display-movement. The female would run for a short distance to one side on straightened ambulatories, with both chelipeds raised and moving out and in again once or twice. Then the female would stand still, dropping her chelipeds and bending her ambulatories slightly, before repeating the movement. The

display-movement of the U. marionis females did not appear to have any aggressive significance since it was used only during courtship and generally in order to attract the males, but it was reminiscent of the threatening-gesture shown occasionally by U. inversa females towards other females.

Again during both February and April-May, certain male individuals were observed, each standing motionless at his burrow-entrance, with his ambulatories bent. Such a male was apparently straddling the mouth of his burrow, for his two sets of ambulatories were supported, one on either side of the entrance. The major cheliped of such a male was usually held straight out to the side, slightly raised and with the claw partly open, but occasionally it was simply held in the position of rest. When a female crab approached such a male, the tips of his now straightened ambulatories would immediately begin to move up and down while the individual remained, nevertheless, on more or less the same spot. At the same time, he would beckon wildly once or twice with his major cheliped, using the same movement as for threat-display, except that he did not run about from side to side. One typical male was seen to remain at the entrance to his burrow for about half an hour in a characteristic, motionless statuesque pose, and he disappeared into his burrow only after a sudden movement on the part of the observer had disturbed him. After a while, he re-emerged from his burrow and once more took up a position at the entrance but, on this occasion, he moved his bent major cheliped very slightly upwards and in again, repeating this rather slow, lethargic, indefinite movement several times before pausing. The claw itself was ^{a little} open, and the slightly bent ambulatories were moving up and down individually, some even leaving the ground for a few seconds at a time. Male individuals were constantly seen rushing

at female crabs, often from some distance away, and chasing them to their burrows at a speed much greater than was ever observed in *U. urvillei*. Should such a female retreat into her burrow, a habit which was not very common however, the male concerned, instead of waiting for her to emerge once again, was frequently seen to turn his attention immediately to other females. On the whole, during the breeding-season, the females of this species appeared to be far less timid than those of *U. urvillei* and seemed to be trying very hard to attract the attention of the male individuals. Occasionally one or two particularly bold females were seen to behave rather oddly, and appeared to be trying to entice male crabs to come towards their burrows. Such a female would run a short distance towards a male individual, then run a slightly longer distance back towards her burrow, then a short distance towards him again, and a longer one back, and so on. Frequently, the male concerned would respond by gradually following her to her burrow, and certainly any partial mount that was observed did take place at the entrance to the female's burrow. As far as is known, this means of attracting the male to the female burrow has not been recorded by any other worker on *Uca*. As has already been suggested, the female display-movements and the adopting of statuesque poses by many females at the entrance to their burrows may also be means of attracting the males. Particularly in April-May, the females appeared to be in a state of high nervous tension, which was very noticeable in their behaviour towards one another. Occasionally, they were seen to approach one another on the very tips of their straightened ambulatories, their two small chelipeds raised and perhaps, moving outwards and in again, from time to time. This movement did not appear to be a form of threat and, usually, the females would simply scamper past one another.

Now and again, however, two such females would approach one another rapidly and, at the entrance to one or other of their burrows, one individual could be seen to climb a little way on top of the other. In each of the few cases observed, the two crabs were facing in opposite directions and, by means of their hindmost pairs of ambulatories, a certain amount of mutual stroking was taking place. After a few seconds, the two would separate, the mounting female generally scampering off hurriedly, and the other hastily entering her burrow. This exceptional behaviour of the female individuals was possibly due to the fact that they were somewhat "frustrated". In spite of the fact that the breeding-season of this species was virtually over, the sexual drive of the females, like that of many of the males, was nevertheless still very strongly activated, and the thwarting of this drive was due to the fact that there was no longer sufficient opportunity for normal copulation to take place.

In this species, a far greater number of instances of males partially mounting females was observed than was ever noticed in *U. urvillei*, and the *U. marionis* individuals were behaving far more tensely than was ever observed amongst individuals of *U. urvillei*. Nevertheless, apart from the large number of differences noticed between the two species, many similarities were also detected. In both species, for example, a male individual would generally court more than one female in quick succession, and a female would allow herself to be stroked by more than one male, within a relatively short period of time. A male crab would either chase a female to her burrow or follow her there. At the entrance to the burrow, the female would generally pause, unlike the females of *U. urvillei*, and would allow the male to mount her partially. Should such a female by any chance

disappear into her burrow, she would usually re-emerge almost immediately. The female would nearly always face towards her burrow, and the male would climb partly on her carapace, usually facing in the same direction as the female, but sometimes in the opposite direction. Since the *U. variolus* individuals were so terribly tense and unable to remain in one position for any length of time, such a partial mount would generally last for only a few seconds, but a few rather unusual mounts, one or two of which will be described later, lasted up to about five minutes each. With his ambulatories and minor cheliped the male would gently stroke the ambulatories, carapace and perhaps even the eyespots of the female, while he would generally rest his bent major cheliped across her carapace. As in *U. urvillei*, the ambulatories of the female were occasionally seen to leave the ground momentarily during the stroking-process. Sometimes the male would end the matter by dismounting suddenly, but it was usually ended by the female. She would suddenly move down into her burrow, leaving the male to scamper off, often with his whole body quivering very slightly, but more so than was ever noticed in a *U. urvillei* male. Here and there, a large male was noticed chasing a smaller male off the carapace of a female which he had mounted, and, unless the female concerned ran into her burrow, such a male would generally proceed at once to mount her himself.

During April-May, a particular male was observed to mount a female and to sit squarely on her carapace, but facing in the opposite direction. With his ambulatories, he gripped her firmly but, from time to time, he stroked her with his minor cheliped and ambulatories. This case was particularly interesting, because the flap-like abdomen of the male kept moving out and in fairly regularly throughout

the mount. The male held this position for about five minutes, when he suddenly dismounted and hurried off in a very tense manner, and the female disappeared immediately into her burrow. On another occasion, a large female was observed at the entrance to her burrow leaning backwards with a smaller male individual leaning against her. The narspace of the female was resting on the far edge of the burrow, and she was supported by only her last pair of ambulatories. With the remainder of her ambulatories, and with her two small chelipeds, she gripped the male individual. The male crab was likewise supported by only his last pair of ambulatories, the other pairs being used in their turn, together with his minor cheliped, to grip the female, while the major claw was simply held at rest against the female's body. The ventral surfaces of the two crabs were applied to one another, and the posterior ends of both of their bodies were obscured by the edge of the burrow nearest to the observer. A certain amount of mutual stroking was noticed, and the two crabs held this position for a little over five minutes, when the male slowly disengaged himself and moved off. Although the instances of "love-play" described above were very typical of the way in which the *U. marionis* individuals were behaving at the time, nevertheless only those cases in which a male had partially mounted a female and was facing in the same direction as herself, could be described as preliminary stages to copulation. As in *U. urvillei*, no actual phases of copulation were ever observed in this species, probably because, even in February, the breeding-season was nearing its close. As in *U. urvillei*, the ovaries of the *U. marionis* females collected during February were found to be extensive and to have large ova, and the females themselves were ovigerous, so that copulation would have been quite impossible during this month. Again, since the breeding-season was so nearly over, the eggs were found to be in a fairly late stage.

of development. Female individuals collected in April-May, when the breeding-season was virtually over, were found to have very undeveloped ovaries, so that copulation at this stage would have served no purpose, and this was probably the reason why no instances of actual copulation were ever observed during these months.

The male individuals of two of the five *Inhaca* species, namely *U. marionis* and *U. urvillei*, were found to have a highly characteristic, striking nuptial dress, which is retained throughout the breeding-season and which plays a definite part in attracting individuals of the opposite sex during courtship. In contrast to these two species, starting males of twelve of the *Uea* species investigated by Grane (1941) at Panama all show a nuptial colour-change which is again retained throughout the breeding-season, but in which the colours show a definite diurnal variation. The individuals, after emerging in the morning, change from a dull to a striking colouration, and, whereas in the two *Inhaca* species it is chiefly the carapace which changes colour, in the Panama species the carapace, major cheliped and ambulatories of the individual are all affected by the colour-change. Grane found, too, that dryness and sunlight seemed to be equally important in effecting colour-change and that the most specialized forms of *Uea* crab had the most arresting colouration, often possessing a completely white carapace. Grane noticed differences in the methods of display of the different species. One of her species, *U. saltitans*, is particularly interesting in that the individuals seem deliberately to mount slight elevations in order to display to better advantage. The *U. chlorophthalmus* males and *U. marionis* females at *Inhaca* also tend to stand on raised ground in order to make themselves all the more

conspicuous. *U. saltitans* is found living in open, sticky mudflats, and it is a highly specialized form of *Uca* crab. Grane found that related *Uca* species have fundamental similarities of display in common, and that series of species which showed progressive specialization of structure generally showed similar progression in display. Pearse (1912) noticed that the males of certain *Uca* species in the Philippines would hold statuesque poses during display, the major cheliped being held out to the side or raised high above the head for minutes at a time. Individuals of *U. pugilator*, for example, appeared to alternate simple waving of the major cheliped with such statuesque poses. Individuals of *U. mordax* would also freeze in this way, holding the position for three or four minutes at a time. Male individuals of all the *Inhaca* species, except *U. urvillei*, were seen at the mouth of their burrows, for periods which varied in length from one species to another, to hold such statuesque poses, with the major cheliped raised, or, at least, to stand motionless with the major cheliped held at rest. In some of the *Inhaca* species, too, females were also observed in statuesque poses, again at the entrance to their burrows. "Revolution", as described by Grane, was rare in *Inhaca*, and apparently the few male individuals showing it all belonged to *U. merionis*.

(6) CLAW-WAVING.

Various workers on *Uca* have expressed their views on the functions served by the waving or beckoning-movements of the major cheliped of the male, a phenomenon which is generally referred to as claw-waving or claw-beckoning. For example, Verwey (1930) claims that claw-waving is used exclusively as a means of threat, to warn intruders off the territory of the beckoning individual. Grane (1941), however, while admitting that the waving of the major cheliped is used as a means of territorial defence and, hence, as a means of delimiting the territory of each individual, asserts nevertheless

that claw-waving plays a major rôle in courtship, it being the chief method of attracting individuals of the opposite sex. Crane points out that this latter function is especially noticeable in those species in which waving is limited to the reproductive season. Peters (1955) describes the variations in the methods of claw-waving shown by the different species of *Uca* and *Mimada* investigated by him. He found that the method of waving varies from one species to another, particularly in the duration of the movements involved, but, within any one species, the method of beckoning is remarkably stereotyped. He asserts that claw-beckoning in *Uca* crabs is chiefly a means of territorial defence, because the individuals occur generally in very dense populations and, not only do they spend a long period of every day out of their burrows, feeding, but they have an unobstructed view of one another on the feeding-grounds.

The different methods of claw-waving, associated with both threat and courtship, as shown by the different *Inbaca* species of *Uca* have already been described under the relevant headings. Amongst these species, however, various modifications of the phenomenon of claw-waving were also observed and are discussed below.

(a) Synchronous claw-waving in *U. annulipes*.

A peculiar type of rhythmic claw-waving, involving small groups of individuals, was first noticed in February 1955 at both the Saco and the South Swamps. It was confined solely to males of *U. annulipes*, and it appeared to be at its peak during February, when it was mid-summer. For every *U. annulipes* population in both the swamps seemed to have a few groups of synchronous claw-wavers. During April-May when the weather was cooler, synchronous claw-waving was again noticed at both the swamps, but to a lesser extent, the number of synchronising groups noticed in any one *U. annulipes* population being

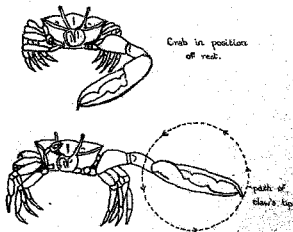
considerably fewer, and the synchronous waving itself being, generally speaking, somewhat less intense. As a result of this, most of the observations on synchronous claw-waving were made during February.

Synchronous claw-waving was apparently performed by male crabs which, when they were not occupying their time in this way, were busily feeding or showing independent claw-waving, usually to threaten other males but occasionally, in February anyway, to attract the attention of passing females. Apart from being at its maximum during the warmer months of the year, synchronous claw-waving shows also a daily peak, which is reached during the hottest part of the day, the waving being at its most intense during these hours. Early in the morning and in the late afternoon, there are fewer groups of synchronous wavers to be seen, and most of the claw-waving which does take place at these times is performed by scattered males independently of one another. There is always a greater number of waving groups in sunlit areas than in the shade where, as a general rule, the individuals are definitely rather sluggish, being far less active than those exposed to the sun.

Synchronous claw-waving generally starts when one or rarely two *U. saxatilis* individuals begin to beckon with their major chelipeds, occasionally as a reaction to a passing female but nearly always for no apparent reason. Almost immediately, one male after another in the vicinity of the beckoning male gradually begins to wave his major cheliped until there is a small group of individuals, moving automatically in unison, the movements of their bodies and chelipeds being synchronized to a remarkable degree. The individuals in each group appear to be in some way lulled by the rhythmic movements of their fellows, for they generally continue to wave thus for an average of about ten to fifteen minutes. There are usually about five to seven crabs in a group, and

the individuals may all face the same way or in different directions, some even standing back to back with one another. Very occasionally, when a particular female is the "trigger" setting off the claw-waving mechanism in the first male individual, she becomes more or less surrounded by a ring of synchronising males. Such claw-waving, however, invariably continues long after the female has moved away, and new individuals who never even saw the female responsible may join the group. Frequently, there are as many as ten small groups of synchronous wavers in a small area, and these groups usually overlap one another to a certain extent. For example, a particular male involved in the synchronised waving of one group may suddenly and for no apparent reason become involved in the synchronised waving of a neighbouring group. Moreover, adjacent synchronous groups may gradually merge together to form a larger group, in which all the individuals gradually begin to wave their claws in unison. The individuals do not appear to feed whilst they are engaged in synchronous waving, but an individual in a group may gradually stop waving and, possibly, move a short distance away in order to feed. If such an individual should by any chance move into the midst of a neighbouring group of synchronous wavers, he will generally stop feeding almost at once and automatically join in the waving of this group. The fact that the individuals comprising a group move about and change their group from time to time indicated another way in which overlapping of the groups takes place. Each individual tends to alternate spells of synchronous claw-waving with bouts of feeding. As gradually as it begins, synchronous claw-waving ends. Just as one individual after another gradually takes up the movement until a group is formed, so one individual after another gradually stops waving, again for no apparent reason. Although the majority of synchronous claw-wavers are adult, some rat or small young forms were noticed in many of the groups.

The claw-waving movements of each individual in a synchronous group are essentially similar to the normal beckoning-movements used by a male when threatening another male or attracting the attention of a passing female. The movements involved, however, are even more deliberate than those used in courtship-display which, as has been previously pointed out, involves movements which are not only faster and more jerky than those of threat-display, but which are also more definite and of a higher intensity. The movement of each individual in the group starts with the position of rest; that is, the ambulatories are bent slightly and the major cheliped is held bent and in the normal plane, with the claw itself pointing slightly forward. The cheliped unbends and is stretched out sideways to the very fullest extent and, with the cheliped held in this position, the crab gives a pronounced jerk or jump, generally moving a short distance to one side but, very occasionally, landing on the same spot. Next, while raising himself on to the tips of his now straightened ambulatories and lifting his minor cheliped, the individual raises his major cheliped as high as possible so that the claw is pointing upwards, then swings it first round and in towards his body and finally out to the side again, in a smooth, continuous movement. As the major cheliped is raised to its highest point, a few of the ambulatories on the side of the major cheliped may even be lifted momentarily from the ground. As the major cheliped is restored to its position out to the side of the individual, the minor cheliped is lowered and the ambulatories bent slightly once again.



After each beckoning-movement, there is a definite pause of about a second or two, after which the crab generally jerks once again, this time usually to the side opposite but occasionally to the same side as previously, and then the whole claw-beckoning movement is repeated. The individuals in a synchronous group generally keep nearly perfect time with one another, but occasionally the beckoning movements of individuals tend to overlap one another very slightly, one individual starting to move his major cheliped before another which, in its turn, starts the waving-movement before yet another individual, and so on. On the whole, too, the crabs all jerk at approximately the same instant, and they generally all jerk to the same side, whether or not they are all facing in the same direction.

Since it is a phenomenon which is correlated with temperature, synchronous claw-waving can best be described as a physical expression of an excess of energy, which has resulted from the fact that *Uca* is a sun-loving genus. Why this surplus energy finds expression in synchronous claw-waving in one species only is not clear. *U. annulipes*, however, is the species longest exposed to the sun every day,

and this may explain why it is the only species showing synchronous claw-waving.

(b) Special claw-waving in *U. annulipes*.

At the Saco Swamp, and only during April-May, a few male *U. annulipes* individuals were very occasionally seen to alternate their normal, non-synchronous claw-beckoning movements with a special method of apparently low-intensity claw-waving. Such a male would suddenly, and for no apparent reason, stop waving his major cheliped and instead would begin to move it very slightly outwards and in again, while holding it bent and in the normal plane. This movement was inconspicuous and irregular, and was repeated only once or twice in between normal claw-waving movements. It was reminiscent of normal claw-waving in *U. inversa* males, as described under "Fighting".

(c) Special claw-waving in *U. chlorophthalmus*.

During February only, a special method of claw-waving was noticed amongst several male crabs in the shade of Region B of the Saco Swamp, at a time when very little normal claw-beckoning was noticed. The major cheliped of such an individual was apparently again held in the normal plane and was moved slightly away from the body and then inwards again in a slow, even, non-jerky movement, which gave one the impression that the crab was rather sluggish or lethargic. The movement was repeated several times before pausing and, during such a pause, a crab would often resume normal feeding. Although there was occasionally a female in the vicinity, such a male generally performed this special movement for no apparent reason. The movement reminded one most of that shown by *U. urvillet* males and which has been described under "Fighting". A few of these crabs were collected and kept in captivity and once again this particular type of claw-waving was noticed, but to a lesser extent than in the field.

(d) Special claw-waving in *U. marionis*.

Again in February only, males of this species were observed beckoning with their major chelipeds for no apparent reason. The movement was precisely the same as that used in the threat and courtship of this species and hence has already been described under the relevant headings.

(e) Special movement of the claw in *U. urvillei*.

A special movement of the claw of the major cheliped was noticed amongst a few males of this species, once again only during February. Such a male would suddenly stretch open the claw of his bent major cheliped to its very fullest extent, for no apparent reason. Very occasionally, the crab would straighten his major cheliped and would hold it out to the side of his body, before opening the claw. After a few seconds, the claw is relaxed again and, if necessary the major cheliped is bent into its normal position once again. This movement was apparently never used during threat or courtship.

It would seem, then, that the major cheliped of male *Uca* crabs is an organ of expression. It is an organ in which energy finds various outlets and which is hence made use of for various purposes, of which threat, fighting and courtship are the most important. As has already been suggested, *U. annulipes* is the species which is longest exposed to the sun every day, and it is hence the most active species generally, and spends the longest period of time every day in claw-waving.

(7) DISPLACEMENT ACTIVITIES.

Tinbergen (1952) has described a displacement activity as "an activity belonging to the executive motor pattern of an instinct other than the instinct(s) activated", and,

according to Bastock, Morris and Moynihan (1953), such activities would seem to take place in two quite different situations: "(1) Displacement activities may be performed by an animal in which two or more incompatible drives are strongly activated. Each drive prevents the expression of the other(s). (2) Displacement activities may also be performed by an animal in which one drive is, at the same time, both activated and thwarted."

Displacement activities have been reported for various vertebrates, especially for fish and birds. Morris (1954), for example, recently described the displacement activities of the zebra finch, *Poephila guttata*.

To the best of the writer's knowledge, no case of a displacement activity has yet been recorded for an invertebrate. However, the present study of the behaviour of the Inham species of *Uca* revealed a number of instances of displacement activity. These activities were noticed in all five of the species and, in each case, the activity involved was that of displacement feeding.

The normal feeding-process of these crabs has already been described, and it will be remembered that the male individual uses his spooned minor cheliped exclusively, and the female her two small chelipeds more or less alternately, for scooping up mud from the ground.

(1) Displacement feeding as a result of a conflict of incompatible drives - the drive to attack and the drive to flee - was noticed in the following four species: *U. annulipes*, *U. chlorophthalmus*, *U. marionis* and *U. urvillei*. While protecting their burrows from male intruders or being threatened by superior males, and especially between bouts of actual fighting, male crabs were often seen to be feeding rather "agitatedly". Such individuals appeared to be highly "nervous", the scooping movements of their minor cheliped

being far more frequent and far less deliberate than those of normal feeding. During displacement feeding a negligible quantity of food actually seemed to reach the mouth - not sufficient for any sand pellets to be formed. Often the minor cheliped would simply move up and down, as in normal feeding, but making no contact whatsoever with either the ground or the mouth. In the field it was noticed that the majority of individuals of all the species showing displacement activity were males. It is a fact that female *Uca* individuals are, generally speaking, rather timid, for possessing no major cheliped - they are ill-equipped for fighting. If threatened by a male, they can usually manage to escape by scurrying off to disappear down their burrows; that is, in such a case, only their escape-drive is stimulated, so that no tense conflict of drives is involved, and hence, no displacement activity is produced.

(2) Displacement activities due to the simultaneous activation and thwarting of the same drive were observed in *U. marionis*, *U. urvillei*, *U. annulipes* and *U. chlorophthalmus* during their respective mating seasons. This type of displacement feeding was particularly noticeable in *U. marionis* and *U. urvillei*, for these species were observed when their breeding season was far advanced. *U. annulipes* and *U. chlorophthalmus*, however, were under observation when their courtship was only in its incipient stages, so that displacement activity was noticed only occasionally. Generally speaking, during the breeding season, the approach of a female frequently seemed to stimulate a male, causing him to beckon with his major cheliped several times in quick succession, in a manner characteristic of his species. In *U. marionis* males, especially, such courtship-display often appeared to become very intense, with such beckoning individual standing on the very tips of his ambulatories

and, perhaps, running a short distance to the left and then to the right, repeatedly, between individual beckoning movements. Frequently a female would appear to respond to such a display by leading the male to her burrow and, perhaps, by allowing the male to mount her partially and stroke her carapace. Now and again, however, the display of a male crab was ignored by the female, who either continued to feed quite normally or disappeared temporarily down her burrow. In such a case, if the thwarted male were sufficiently aroused sexually, he would frequently begin to show displacement feeding, until the female concerned took notice of him, either by stopping her feeding or by reappearing from her burrow, or until, perhaps, the approach of another female distracted his attention. Thus, periods of displacement activity were often found alternating with periods of intense courtship display.

Under laboratory conditions, displacement feeding was observed in *U. inversa*. Since, in the field, the burrows of this species are rather widely spaced, fighting over the ownership of territories is unnecessary and, therefore, relatively rare. Hence, displacement activities are also at a minimum. However, it appeared that several *U. inversa* individuals, confined to a tank too small for their number, became unnaturally aggressive towards one another. Of these, one female was seen to be performing displacement feeding - the one and only case of a displacement activity observed in this particular species. The female concerned appeared to be trapped in a corner, away from her burrow, and completely surrounded by four males. She ran about "nervously", trying unsuccessfully to make her escape, and even attempted to climb the right side of the tank, falling down again and again. Finally, she began to feed, in a highly "nervous" fashion, and, since her shellpods appeared

to be scooping up no mud whatsoever, it appears that this must be yet another case of displacement feeding.

SUMMARY.

Five species of *Uca* crab - *U. annulipes*, *U. inversa*, *U. chlorophthalmus*, *U. marionis* and *U. urvillei*, - were studied in mangrove swamps on Inhaca Island and on the mainland of Mozambique. Individuals of all the species were also observed while in captivity. The feeding-grounds of these five species are on the landward and seaward margins of the swamps, the mudflats of which are submerged during high tide. In the case of *U. marionis* and *U. urvillei*, which are confined always to the seaward side of the swamp, this submersion is semi-diurnal, while, in the case of most of the *U. chlorophthalmus* feeding-grounds, it is semi-diurnal, except during the lowest neap tides. The *U. annulipes* habitat is variable in that, in some localities, the submersion is semi-diurnal, while, in others, there is no submersion for anything up to eight days at a time during periods of neap tide, when *U. annulipes* individuals may be seen temporarily to migrate en masse towards the lower-lying parts which are still submerged. *U. inversa* has a habitat on the landward side of swamps on drier mudflats which are submerged only during the highest spring tides. Although the five species are sympatric, they have each a preference for a particular ecological niche. In certain localities, however, populations of the different species may overlap one another, to a greater or lesser extent, this intermingling being confined, generally, to two species although, sometimes, three species may be involved.

The feeding-method of all the species was found to be typical of *Uca* crabs generally. *U. inversa*, however, has a more efficient method of feeding, probably because

the individuals of this species have the shortest total feeding-period of all the *Urhaca* species.

U. marionis and *U. urvillei* feed during the warmest part of the day, on very wet mud, which is wetter in the case of *U. marionis*. The feeding-ground of *U. chlorophthalmus* is shaded, and the mud is somewhat drier. The *U. chlorophthalmus* crabs also feed during the warmest part of the day, except during those periods when their feeding-ground is not being reached by floodwater, and, at such times, the individuals remain in their burrows. The feeding-grounds of *U. annulipes* show great variation in their degree of wetness - that is, they vary from the dry, sandy mud on the landward side of swamps to the black, soggy mud in the interior of swamps, and they may even be found in shallow standing water left by spring tides. Individuals of this species feed during most of the day, except during periods of low neap tides, when feeding is limited to early morning and, perhaps, to the late afternoon. *U. inversa* is limited to drier, sandy mud, and, only after high spring tides, the individuals feed during most of the day. During neap tide periods, however, a limited amount of feeding is noticed around the shaded bases of young mangroves.

The burrows of the five species are situated in their respective feeding-grounds, except, sometimes, in the case of *U. annulipes*, the individuals of which species, in certain habitats, make irregular journeys, to and fro, between their burrows and freshly - moistened mud. The shapes of the burrows vary from one species to another. In drier, sandy flats, the burrows are deeper, as is the case for *U. inversa* burrows (2 7" deep). In wet mud, the burrows are more oblique and less deep, e.g. *U. marionis* and *U. urvillei* burrows (2 5" deep). The *U. chlorophthalmus* burrow has a distinct rim of mud round the entrance, of which the crab makes use during courtship.

The following general habits and behaviour-patterns of the five species were studied: - cleaning, recognition, timidity, fighting, courtship, special claw-waving and displacement activities. All the crabs appear to respond to visual stimuli, especially moving objects or shadows. The males, moreover, seem to have no difficulty in recognising the females of their species. *U. inversa* is the most timid species, while *U. marionis*, due to the nature of its habitat, appears to be the least timid. Intraspecific fighting is far more common than fighting between the species. Males are considerably more aggressive than females, and most of the hostility centres around the ownership of burrows. Threat is far more common than actual fighting, and the activities connected with both involve the use of the major cheliped. Each species has a special mating-period, but these periods overlap to a large extent. The males of only two species - *U. marionis* and *U. urvillei* - adopt a nuptial dress during their respective mating - seasons, and *U. marionis* is the only species which moves to a special breeding-ground. *U. marionis* is unique, too, in that, at the height of the breeding-season, the females appear to do all in their power to "entice" the males to the mouth of their burrow, and, very occasionally, a thwarted female may even attempt to mount another. No case of an actual copulation was ever observed in any of the species, although a fair number of males of both *U. marionis* and *U. urvillei* were seen partially mounting females. In male crabs, claw-waving plays a definite rôle in both threat and courtship, and the movements involved vary from species to species. A special type of claw-waving, however, was noticed in several of the species, and it appeared to serve no particular purpose. During the warmer

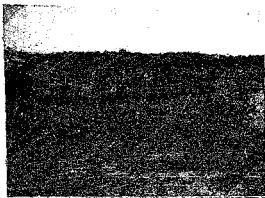
seasons of the year, *U. annulipes* males show widespread synchronous claw-waving, which reaches a peak towards the middle of every day. This highly specialised form of claw-waving is probably due to the excess energy of this species which results from the individuals spending the most time out of their burrows, exposed to the sun. What appeared to be genuine displacement activities were noticed occasionally amongst male *Uta* crabs, either as a result of a conflict between the drive to attack and the drive to flee, or as a result of the simultaneous activations and thwarting of the sexual drive. The displacement activity in each case took the form of an incomplete feeding-movement. The only case of a displacement activity shown by a female was observed in a laboratory tank.

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PLATES.

PLATE I



1



2



3

Region A
on a

PLATE I.

SUBMERSION OF A FEEDING GROUND.

Fig. 1. A typical *U. annulipes* habitat in Region A of the Saco swamp. Time 12.15 p.m. and a day with high tide at 3.30 p.m.

Fig. 2. Same locality, 4.0 p.m.

Fig. 3. Same locality, 5.0 p.m.

PLATE II



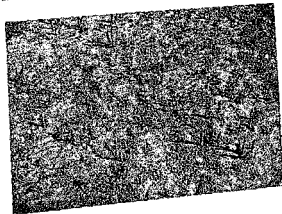
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the water in
the corner of
the field.

the ground
level, i.e.
the field.

PLATE II.

THE DEGREE OF WETNESS OF MUD IN RELATION TO
DISTANCE FROM THE SEA.

- Fig. 1. The area connecting Regions B and C of the Saco swamp, exposed during low tide.
- Fig. 2. Near the above locality, submerged during high tide.
- Fig. 3. *U. annulipes* individuals feeding amongst *Avicennia* roots, on wet mud, nearest the water, i.e. the top left hand corner of Fig. 1. Note the many *Terebralia*.
- Fig. 4. *U. annulipes* individuals feeding on drier mud, farther from the water edge, i.e. adjacent to the locality of Fig. 3.

PLATE III

at southern end
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 ith Avicennia

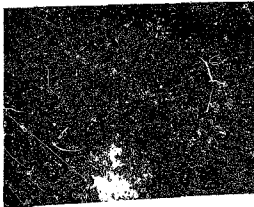
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PLATE III.

HABITATE OF *V. ANNULIPES* .

- Fig. 1. Extensive *Avicennia* root area at southern end of Region C of Saco swamp, exposed during low tide. Uninhabited by *Vsa*.
- Fig. 2. Feeding ground on a beach of the North swamp with wet mud densely covered with *Avicennia* roots.
- Fig. 3. Feeding ground on the beach of Region D of the Saco swamp, below the *Avicennia* root area with fairly dry sand also inhabited by a *Dotilla* species.

PLATE IV

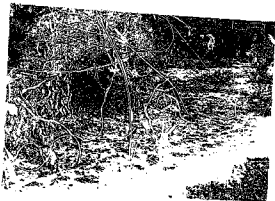
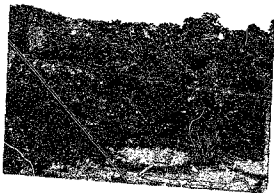


PLATE IV.

HABITATS OF *U. ANNULIFES*.

- Fig. 1. Feeding ground on drier sand at the northern end of the South swamp, adjoining a *Cordia* patch on the landward side of the swamp.
- Fig. 2. Feeding ground on fairly light dry sand within the fringe of *Avicennia*, in Region of the Saco swamp.
- Fig. 3. Feeding ground on fairly wet sand, within the fringe of *Avicennia* and *Bruguiera* of the North swamp.
- Fig. 4. Feeding ground on very wet black mud at northern end of the South swamp.

PLATE V

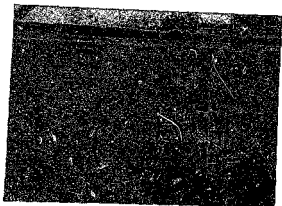
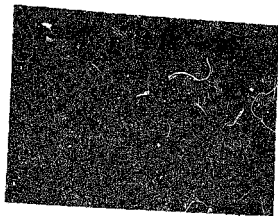
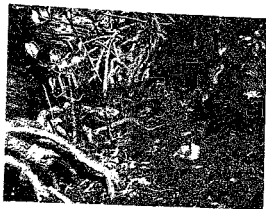


PLATE V.

LOCALITIES IN WHICH MASS MOVEMENT OF U. ANNULATUS
WAS OBSERVED.

- Fig. 1. The beach at the end of the cross-path
in the Mainland swamp.
- Fig. 2. Sandbank alongside Region C of the Mass
swamp, exposed during low tide.
- Fig. 3. The eastern part of the open flat at the
northern end of the South swamp.

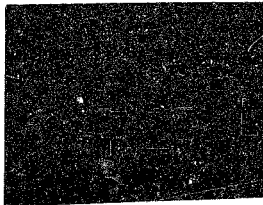
PLATE VI



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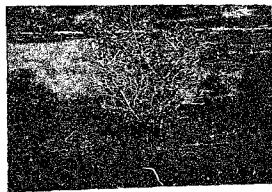
on main pathway
re the population

PLATE VI.

HABITATS OF DIFFERENT SPECIES.

- Fig. 1. Feeding ground of *U. urvillai* on bank of channel at southern end of South swamp.
- Fig. 2. Feeding ground of *U. chlorophthalmus elongatus* the main pathway at the upper end of Region B of the Saco swamp.
- Fig. 3. Feeding ground of *U. annulipes* on main pathway adjoining the above, and where the population density is 50/sq.yd..

PLATE VII



A of the Saco
in the background.
at, with only
but U. inverse
s to the right.
e towards the
base surrounded
e to its burrow.
ellets in foreground

PLATE VII.

A HABITAT OF *U. INVERSA*.

- Fig. 1. The sandy open flat of Region A of the Saco swamp, with the Saco itself in the background.
- Fig. 2. South-eastern part of open flat, with only *U. annulipes* towards the left, but *U. inversa* interspersed with this species to the right.
- Fig. 3. A typical young *Avicennia* tree towards the middle of the open flat, the base surrounded by wetter mud.
- Fig. 4. *U. inversa* male at the entrance to its burrow. Note typical *U. inversa* sand pellets in foreground.

PLATE VIII



1



2



3

PLATE VIII.

cross-path in
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left centre
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PLATE VIII.

HABITATS OF SYMPATRIC SPECIES.

- Fig. 1. The open patch alongside the cross-path in the Mainland swamp, with *U. urvillei* on the extreme left, *U. chlorophthalmus* left centre, and *U. annulipes* to the right.
- Fig. 2. The open triangle of mud alongside the upper end of the channel in the South swamp, with *U. urvillei*, *U. marionis* and *U. annulipes* interspersed.
- Fig. 3. About 200 yds. south in Region C of the Bane swamp, with *U. chlorophthalmus* at the tree edge, left centre; *U. urvillei* at the tree edge, right centre; *U. marionis* in left foreground; *U. annulipes* in right foreground. (cf. Text-fig. 4)

PLATE IX

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at the southern



PLATE IX.

HABITATS OF SYMPATRIC SPECIES.

Fig. 1. The *U. urvillei* habitat at the northern end of the locality shown in Pl. VIII, Fig. 3 and Text-fig. 4.

Fig. 2. The main *U. annulipes* habitat towards the middle of this locality.

Fig. 3. The *U. chlorophthalmus* habitat at the southern end of this locality.

PLATE X

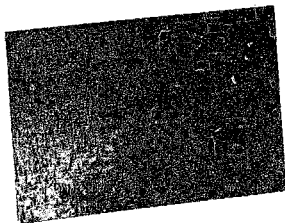
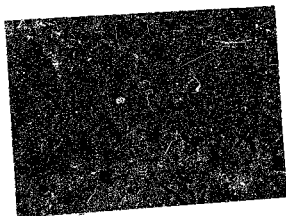
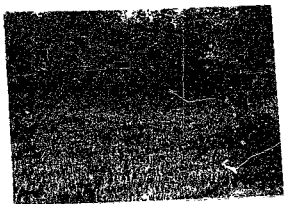


PLATE X.

HABITATS OF SYMPATRIC SPECIES.

- Fig. 1. The main *U. marionis* habitat in very wet mud with standing water. Same locality as shown in Pl.VIII, Fig. 5 and Text-fig. 4.
- Fig. 2. A close-up of the above *U. marionis* feeding ground.
- Fig. 3. Breeding ground of *U. marionis* in drier mud nearer the trees, i.e. in the *U. annulipes* habitat of this locality.

PLATE XI



1



2



3

PLATE XI.

HABITATS OF SYMPATRIC SPECIES.

- Fig. 1. The northern open flat of the South swamp, showing water standing from the previous spring high tide (cf. Text-fig. 5).
- Fig. 2. The same locality, still during the neap tide period, but a few days later, showing mass movement of *U. annulipes* into the wetter mud.
- Fig. 3. The same locality, still later in the neap tide period, showing a few remaining *U. annulipes* individuals on the now drying mud. The *U. invaria* habitat is in the foreground.

PLATE XII



PLATE XII.

HABITATS OF SYMPATRIC SPECIES.

- Fig. 1. To the south-west of the same locality as shown in Pl. XI. The black mud in the background is a *U. annulipes* habitat, while the grey mud of the foreground is inhabited mainly by *U. inversa*, but with a few *U. annulipes* individuals interspersed.
- Fig. 2. Black mud with *Rhizophora* and *Cer tops*, alongside the above, inhabited only by *U. annulipes*.
- Fig. 3. Standing water next to the above, showing *U. annulipes* on black mud. During May 1955 a new colony of *U. chlorophthalma* was found to the right of this area.

Author Gordon Helen R S

Name of thesis A Study Of The Ecology And Behaviour Of Five Species Of Uca Crab. 1955

PUBLISHER:

University of the Witwatersrand, Johannesburg

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