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Combat, display and ritualization in Fiddler Crabs (Ocypodidae, genus *Uca*)

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The principal elements of fighting and display in the genus *Uca* are surveyed from the point-of-view of their apparent evolutionary origins. The components include combat behaviour between males, threat postures, acoustic signals and visual displays. The latter are characterized by rhythmic motions of the large cheliped and other appendages. Combat between males is highly ritualized, with morphological and behavioural deterrents to maximum intensity. When the deterrents are effective the fights are usually without noticeable results. Although serious injury virtually never occurs, when the deterrents are inadequate the loser sometimes gives up his burrow and occasionally does not court for varying periods thereafter. Combat seems to have evolved directly from the decapod motion of grasping combined at low intensities with an appeasement element in which the major cheliped—a releaser of aggressive behaviour—is turned away from the opponent. Threat postures are primarily intention motions of fighting. Both in the burrows and occasionally on the surface stridulation and other acoustic signals are used in threat, courtship or both. Unlike combat behaviour and threat postures, visual display is species-specific. The twenty-odd elements most often occurring in both acoustic and visual display seem clearly to be derived chiefly from feeding, cleaning and threat movements, usually through the intermediary of displacement activities; sometimes the display elements apparently evolved from conflict between feeding and threat tendencies and sometimes from intention motions. Even in species with the most advanced displays, ritualization of some elements is often only partly or temporarily achieved, while the corresponding displacement motion, unaltered and uncomplicated, is frequently elicited. Parallelisms are evident between the courses of evolution in the social behaviour of fiddler crabs and vertebrates.

1. Introduction

Male fiddler crabs have long been famed for their single great claws, which they wield vigorously in combat, threat and courtship. These crabs are without doubt among the best of all invertebrates for ethological study. Their social behaviour is notable for the variety of display, the means of ritualizing combats, and the organization of territorial behaviour. Sixty-two species live accessibly in the warmer parts of the world. All are largely diurnal, active at low tide, often sympatric and always gregarious.

As shown in other contributions to this Symposium, the evolution of any pattern in social behaviour is typically from a variety of sources. In the absence of fossil activities, conclusions can never be proved to the satisfaction of everyone. The sequences often, however, turn out clearly to be formed from pieces of feeding, cleaning, fighting and other patterns, resulting in curious hotchpotches that nevertheless work. Such is the case in *Uca*.

In the course of evolution these pieces of patterns have, with changed functions, become simplified, exaggerated or both. Hence they are termed 'ritualized' in the sense used by Huxley (1914), Lorenz (1941), Baerends (1950) and Tinbergen (1952, 1953). As these pioneers have shown in the study of vertebrates, associated morphological characteristics may also be enhanced by increased size, altered shape or changed colour. Through these modifications they are made more conspicuous in visual display or otherwise contribute toward the production of an unambiguous signal in communication.

As in vertebrates, the origins of elements in *Uca* behaviour may be unsuspected when a single species is casually observed. In contrast, when a number of related species, in various stages of display evolution, are studied with care the derivations often become clear. As in other examples, their roots appear most frequently to lie in intention movements and displacement behaviour. These in turn typically result from situations originally involving inadequate motivation, conflict or frustration.

The following report shows striking parallelisms with developments in vertebrates. Without the concept of ritualization in fact, both the motions of the large claw and the subtler movements of other appendages would be unintelligible from the point-of-view of evolutionary biology.

Most of the material in this contribution was presented in the form of a film, accompanied by slides, tape recordings and commentary, at the Symposium. It is based on repeated field trips in tropical America, Africa, south-east Asia and the South Pacific; on studies of *Uca* in large, outdoor terraria at the William Beebe Tropical Research Station of the New York Zoological Society in Trinidad; and on a taxonomic revision of the genus now ready for publication.

All of the material on ritualization and on the control of combat through morphological brakes is published here for the first time. Most of the observations on sound production are also new. General accounts of visual display, of postures in threat and fighting and of behavioural phases were published earlier (Crane 1957, 1958). Sounds were first recorded on tape by Altevogt (1962), Salmon & Stout (1962) and von Hagen (1962).

Because of forthcoming taxonomic changes, specific names in this contribution will be restricted to those of a few examples. Supporting data will appear in a general account of *Uca* soon to be published in book form (Crane, in preparation).

2. Social behaviour in *Uca*

All species of *Uca* live gregariously in the intertidal zone. All are filter-feeders, the food consisting of microscopic organic matter on the surface of the shore. The crabs feed by bringing pinches of substrate to the mouthparts in the specialized minor cheliped. Individuals of both sexes and assorted sizes usually feed close together without agonistic behaviour. Except under special conditions, each crab feeds near the burrow in which it has passed the preceding hours of high tide.

When the tide is low the crabs also repair their burrows. They descend into them temporarily when startled and when driven by heat or dehydration. Current work shows that all fiddlers except the youngest probably make acoustic signals underground when an intruder starts to descend.

In certain behavioural phases males wander widely and aggressively. At these times they attempt to capture burrows from established residents. In still other phases each male defends a definite territory around a particular burrow against other males. The repertory of each species includes threat postures, combat behaviour, acoustic signals and visual display.

The most intense territorial phase is also the time of successful courtship. Visual display is almost always included, and in some species sound production is incorporated. Often the courtship display cannot be distinguished from threat; sometimes it shows further specializations.

The enlarged major cheliped, used in a variety of signals, is a strong releaser for agonistic behaviour between males as well as a stimulant or attractant to the female. In correlation its absence is one of the releasers for courtship behaviour by males.

The following sections suggest the origins of the principal components in combat, in agonistic postures and in acoustic and visual display.

3. Combat behaviour

Intra-specific fighting is widespread among grapsoid crabs and especially in the various genera of ocypodids. In all, except *Uca* males, the chelipeds of both sides are often seized by the claws of the opponent; in intense fighting the protagonists rear up on the posterior walking legs and intertwine the remaining ones; meanwhile the crabs see-saw back and forth, sternum to sternum. In female *Uca* the ambulatories of only one side often interlock with corresponding or opposite appendages of the opponent as the crabs line up beside each other.

In the present contribution fighting between male *Uca* will be the only category considered. In this context fighting or combat is here defined as any behaviour between males in which the major chelipeds are brought into contact.

Like threat postures and unlike display, combat behaviour in male fiddlers is composed of stereotyped postures and motions which show practically no variation throughout the genus and which, with minor differences, are found in their entire range in every species.

The principal postures of combat are shown in figure 1 and illustrate three intensities, as follows.

Position A (figure 1*A*). The major cheliped is wholly or partly flexed, the fingers of the claw being held only slightly apart. This position is characteristic of low intensity fighting, in which each crab pushes with the outer part of the major manus against that of his opponent. In many species the tubercles on the pushing part of the manus are notably enlarged.

The rough tubercles apparently reduce slipping and the consequent easy shift to intense fighting with linked chelipeds (positions *B* and *C*, below). The present position seems quite clearly to be derived from an intention motion of grasping with the claw, which is basic to decapod behaviour (see position 2). To this motion is added an appeasement component, the large chela being turned laterally and its fingers not widely opened. It has already been noted that the large chela is an important releaser for aggressive behaviour. This fact has been shown experimentally by Altevogt (1957) and Salmon & Stout (1962).

The majority of combats are restricted to this stage of low intensity. Most of them break up quickly and inconclusively.

Position B (figure 1*B*). The major cheliped is extended and partly linked with that of the opponent, while the two see-saw back and forth. This position is altogether characteristic of high intensity combat. The tips of the chelipeds very frequently grip the manus of the opponent at the base of the fixed finger (pollex).

It seems certain that morphological specializations of the manus encourage the gripping of the chela tips at this point. In this way they serve as brakes, or deterrents, making less likely the complete linkage to the base of the gape between each pair of fingers. These specializations consist of a variety of pits and small clusters of widespread tubercles in the region of the pollex base, inside and out (figure 2). The oblique ridge inside the manus, present and usually tuberculated in almost all species, appears to act as another barrier to prevent the engaging chela from slipping to a more proximal position.

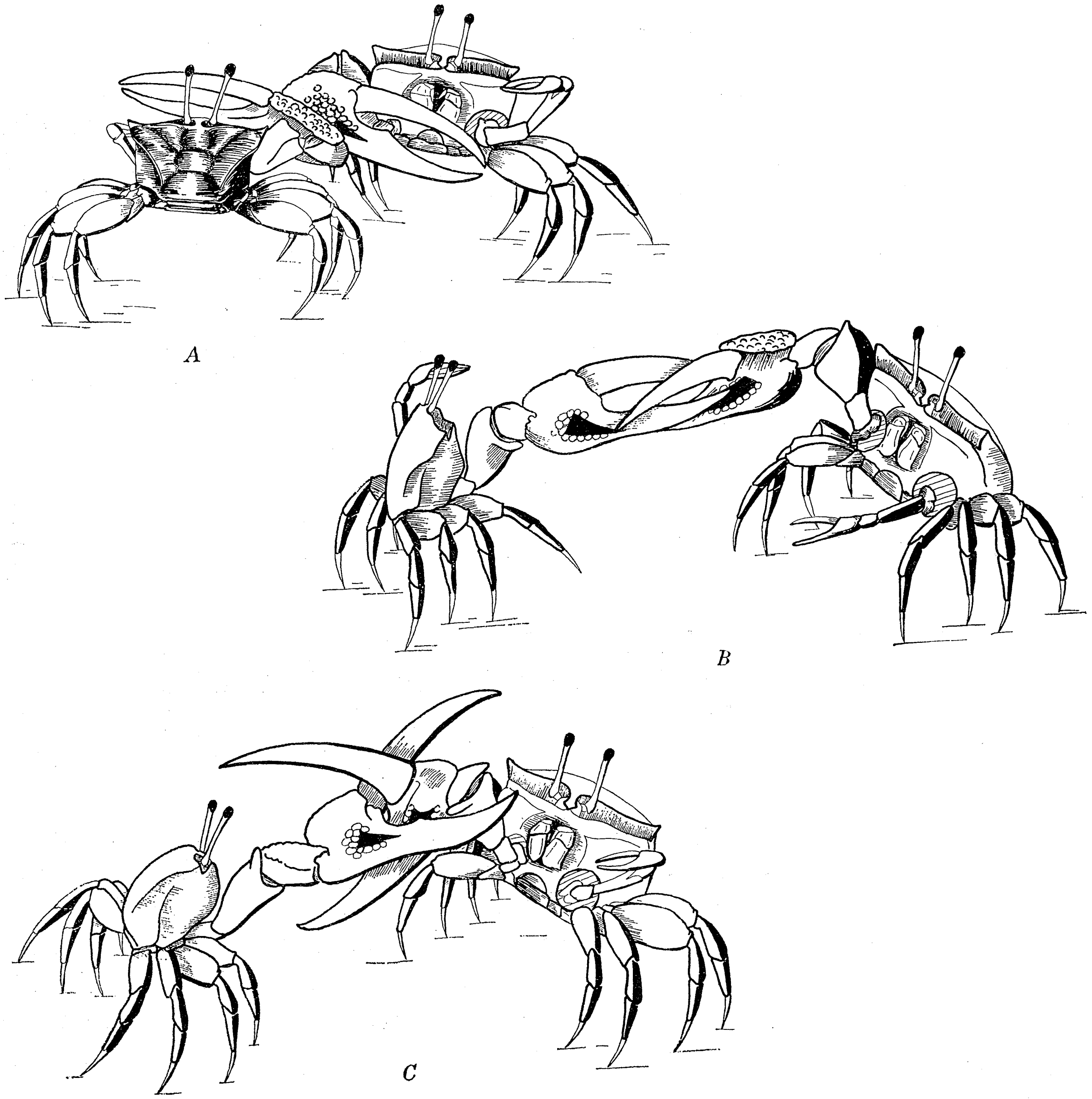

Figure 1. Semidiagrammatic views of three combat positions in fiddler crabs (*Uca*); *A*, low intensity; tubercles outside each lower manus tend to keep chelae from slipping into the positions characterized by linked claws; *B*, high intensity, ritualized, each claw gripping the opponent near base of fixed finger; *C*, highest intensity, the chelae having slipped past the deterrents formed variously by depressions, tubercles and ridges. Deterrents are indicated by circles and black triangles. In actual fighting the boundaries between the positions shown in *B* and *C* are not always distinct.

In a number of specimens in the collections, healed puncture marks are evidence of the actual use of these areas as gripping centres. In other specimens slight abnormal indentations occur, probably resulting from fights soon after moulting, when the cuticle was incompletely hardened. Most numerous are faint scratches in the area. It must be stressed that none of these indications have been found on other parts of the cheliped.

At its best this fighting position, in which the chelae are only partly engaged, shows the highest degree of ritualization. The motions are strongly stereotyped; the tips of the claws not only do not proceed farther than the braking area at the pollex base, but do not even seize it firmly. They simply vibrate the tips gently, first one tip hitting the inside of the opposing claw, then the other touching the outside. No force or pressure is exerted and in combats between well-matched males the crabs do not even see-saw back and forth; instead they stand quietly, vibrating their partly linked chelae for minutes at a time. Sometimes the clicking of the chelipeds can be heard by an observer standing close by, although many species do not measure more than an inch across the carapace. The same well-matched neighbouring males sometimes engage in these ritualized fights on a number of successive days, without any apparent effects, physical or behavioural. Although, as stated above, this behaviour is found throughout the genus, the tendency toward advanced ritualization is found to the highest degree in those species in which other aspects of social behaviour are also advanced. A good example is *U. lactea* (Milne-Edwards).

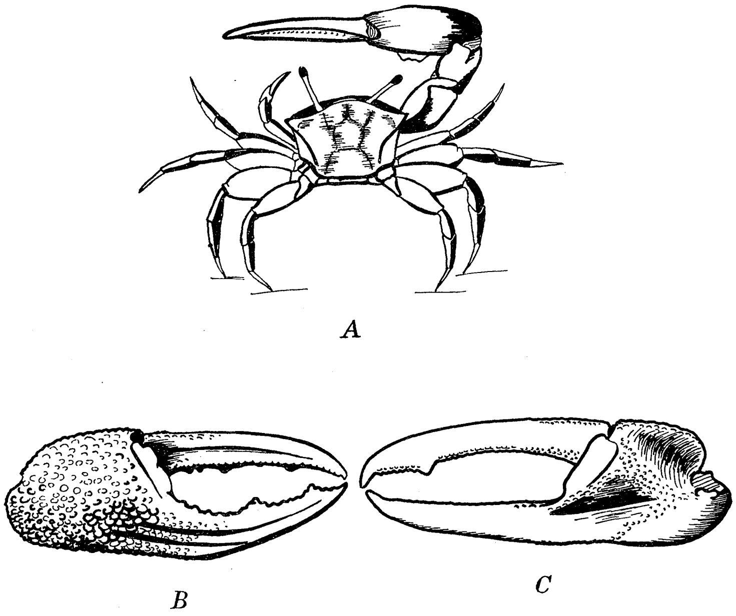

FIGURE 2. Morphological specializations associated with deterrents to highest intensity fights; *A*, dorsal view showing high ridge projecting in profile below folded cheliped at right of claw base; *B*, typical claw, outer view, showing tuberculation; *C*, inner view of a claw, showing triangular pit near base of fixed finger and ridges surmounted by small tubercles.

The fighting behaviour just described seems unquestionably to be derived from the motion made in seizing food, prey or predator, for which in all Decapoda the claws are adapted.

Position C (figure 1 *C*). The major cheliped in this stage is fully linked with that of the opponent, the bases of the claws being in contact. It occurs when the chelae slide beyond the deterrents. Then the fights are often strenuous and prolonged. The opponents seem sometimes to be awkwardly unsuccessful in apparent attempts to disengage. Such combats may well reduce energy for feeding and mating during the remainder of the low tide period. It is at these times too that the rare physical upsets seem most likely to occur, when the weaker crab is flipped upside-down or hurled inches away. Then too, the more usual severe defeats result, although no physical injury is shown. At these times the loser not only retreats but sometimes also gives up his burrow.

In addition, observations both in the field and on marked individuals in terraria show that such defeated fiddlers may lose their display phase for an indefinite time. Certainly the loss lasts for the remainder of the prevailing low-tide period and sometimes for a number of days. Such losers may of course be in the last stages of a current display phase; only extensive future work with marked crabs in a number of species will settle this and related questions.

4. Agonistic postures

Threat postures, like combat components, are not species-specific in *Uca* but take virtually identical forms throughout the genus. Inter-male threat is here defined, for the purposes of this contribution, as any behaviour short of fighting which elicits either similar behaviour or retreat in an attentive conspecific male. The present section concerns threat postures which are largely or wholly static. These characteristics are in contrast to display which is based on rhythmic motions of the major cheliped and which is usually typical of both inter-male threat and of courtship.

In both inter- and intra-specific threat, the basic posture is as follows: the major cheliped in unflexed, directed forward or obliquely outward toward the animal which is the object of the threat. When the threat is straight out at the side or behind the crab, the cheliped is swung out to its maximum lateral extension (figure 4*C*). In all cases the fingers are separated. At its most intensive, whether in forward or lateral threat, the crab raises the body high on the vertically straightened walking legs (figure 3*A*). The obvious morphological specialization is of course the hypertrophy of the major cheliped.

The antithesis of this maximum threat stance is that of submission or appeasement (figure 3*B*), in which the body is held very low, the major cheliped remains flexed and the crab usually moves with the minor cheliped leading. It is characteristic both of individuals defeated in combat and of those in non-aggressive phases when they pass close to aggressive males.

The threat postures, whether the cheliped is directed forward or laterally, are clearly derived from the intention motion of grasping. In the lateral form it is widespread and probably always present in the Brachyura. In *Uca* the minor cheliped sometimes makes a corresponding gesture, as in other crabs, and sometimes does not; much depends on the direction of the potential opponent.

The high-reaching posture is characteristic not only of this relatively static form of threat, but also of displays to be discussed below. It represents the tendency, so widely prevalent in the animal kingdom, to appear larger in any advertising situation, including threat. Similarly, its antithesis, the appeasement posture, is analogous to similar positions, assumed under comparable conditions, in numerous groups of animals.

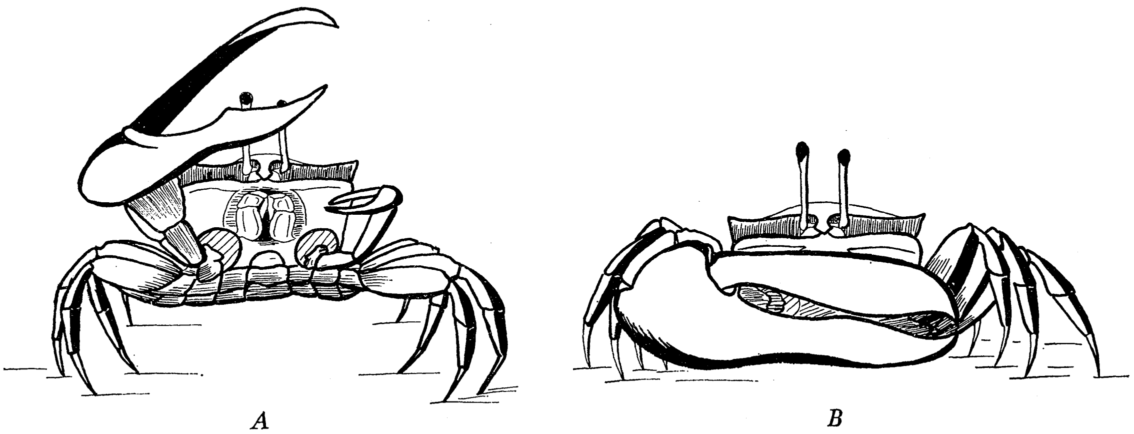

FIGURE 3. *A*, high intensity threat, showing elevation of body on walking legs; *B*, posture of submission and appeasement.

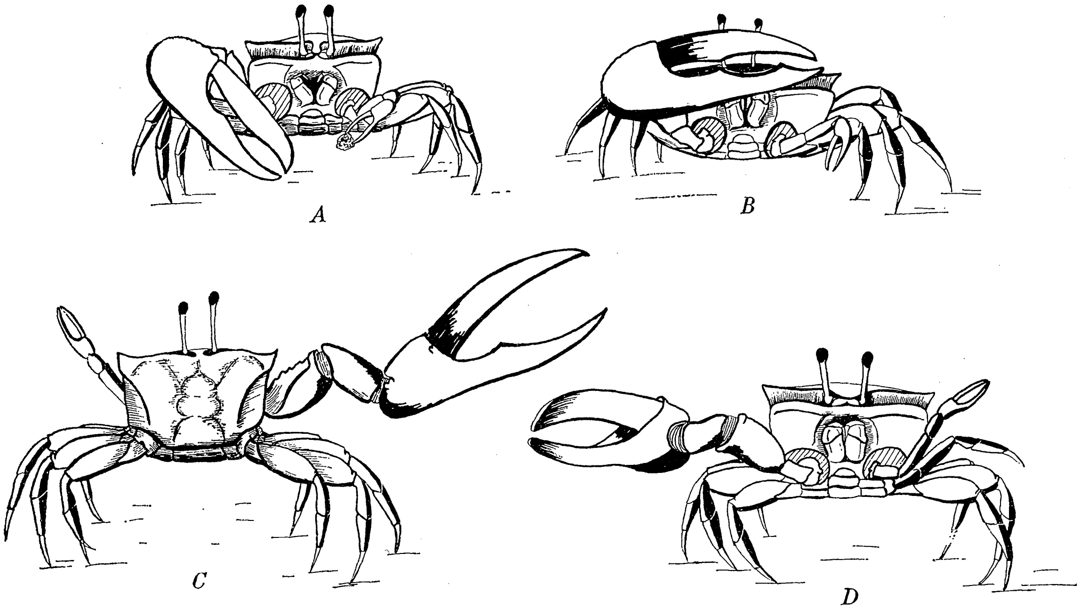

FIGURE 4. *A*, feeding position, showing a pinch of substrate being brought to the mouthparts by the minor cheliped; *B*, vertical form of display, consisting of the elevation of flexed major cheliped; apparently derived from *A*; *C*, lateral threat posture; *D*, lateral extent of lateral display, derived from *C*.

5. DISPLAY

The display of fiddler crabs, in the sense used in this contribution, consists of visual elements, sound-production or both.

In these crabs visual display always includes rhythmic movements of the large cheliped at some point in the display pattern; less conspicuous motions of other appendages are usual accompaniments.

Acoustic display may and often does consist of stridulation and other means of sound production underground; it also often occurs on the surface in association with visual display. Both acoustic and visual forms are characteristic of both threat and courtship behaviour. Frequently the acoustic elements are found on the surface only in threat and conflict situations. Their occurrence underground is not yet well enough known for generalities to be made.

Before listing the chief elements of display and their apparent origins, introductory remarks are needed concerning basic differences in visual display, methods of sound production and the form of displacement activities.

A. *Visual display*

Two basic patterns of visual display have been distinguished (Crane 1957). In the first the major cheliped makes a simple, chiefly vertical gesture or 'wave' (figure 4*B*). In the later stages of courtship the male pursues the female toward her burrow, with or without waving; copulation takes place on the surface of the ground. Vertical display and surface copulation are characteristic of the majority of Indo-Pacific species.

The second group is characterized by a 'lateral wave' (figure 4*D*). The cheliped is unflexed to the side and then raised, rather than vertically elevated in a folded position. Sometimes it completes a circular motion in returning to the rest position. There is in addition a distinct second stage of display, usually elicited by the approach of a female. This phase involves special movements of the appendages, increased tempo of waving and, sometimes, sound production. In the last stage of courtship display the male attracts the female down his own burrow, which he enters first.

Species with intermediate types of behaviour occur. Furthermore, since publication of the above basic differences, additional work has shown me that the vertical type of wave is present at low intensities or among juveniles or in both these situations in every species known to me by more than the briefest observation. Finally, it is now clear that although visual display is undoubtedly species-specific, as long believed (Crane 1941) still it is essential as always in ethology to observe species for long periods under varying conditions. Intensity is of extreme importance; differences result in so many variables, particularly of timing, and in such a continuous range, that it has proved altogether impracticable to set up, for the species descriptions, criteria of 'typical intensity'.

Until electrophysiological work unites with experimental ethology in determining the important releasers among sympatric species of *Uca*, the essential characters of display within a species cannot be precisely described. At present we know from experiment of the existence of two visual releasers. First, the sight of the major cheliped under certain conditions releases aggressive behaviour in males in the requisite physiological phase. Secondly, any crab within a size-range appropriate to the species, without a large cheliped and passing or approaching a male in suitable condition, sometimes elicits courtship behaviour (Altevogt 1957; Salmon & Stout 1962; Crane, unpublished.)

B. *Sound production*

So far very little is known of acoustical behaviour in *Uca* in comparison with our knowledge of visual display. In the single eastern Atlantic species, *tangeri* (Eydoux) and in the western Atlantic *pugilator* (Bosc) the manus of the cheliped is rapped against the side of the burrow and on the surface of the ground in various social situations. Sometimes the vibrations are made at a tempo related to the rhythm of the cheliped in visual display (Altevogt 1962; von Hagen 1962; Salmon 1965).

Recent acoustical work by the present investigator has been chiefly confined to eliciting signals from crabs in their burrows in response to intruders. The signals, in Trinidad during 1964 and in the Indo-Pacific in 1965, were received through a contact microphone and recorded on tape with a battery operated Uher Model 4000. In addition, numerous observations and films have been made of displays on the surface, in which it is obvious that both unritualized and ritualized stridulation play parts, as will be shown below. It is also now apparent that sound is produced in all groups of species in the genus; further study will almost certainly show that every species produces sounds underground and that the sounds may have several functions. It is already clear in a number of species that at least the males produce acoustic signals by at least two methods.

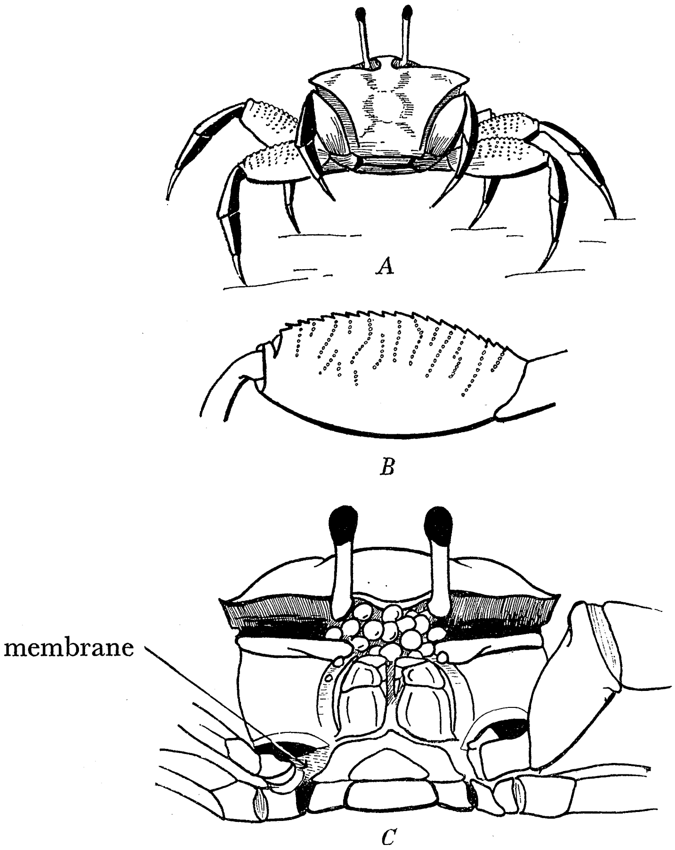

FIGURE 5. Three forms of sound production; *A*, *B*, general form of striations and tubercles on meri of walking legs; used in stridulation by both sexes in many species; *C*, buccal region, showing general locations of bubble emission and of vibrating membrane at base of minor cheliped.

The mechanisms of sound production now known, in addition to the previously reported vibration of the major cheliped against the substrate, are as follows. All result from the above work mentioned in Trinidad and the Indo-Pacific. They consist of stridulation through mutual rubbing of the meri of some of the walking legs (figure 5*A*, *B*); stridulation of parts of the major and minor cheliped against the suborbital and adjacent regions; vibration of membranes at the base of at least the minor cheliped (figure 5*C*) and emission of bubbles from the efferent branchial channels (same figure). In one entire section of the genus another means of stridulation is undoubtedly widely distributed but has not yet been heard, recorded on tape or photographed since field trips with necessary equipment have not been made. The evidence is at present solely indicated by morphological specializations of the cheliped and first walking legs, as well shown in *musica* Rathbun and *terpsichores* Crane. This form of sound production is omitted from the following annotated list of display activities.

Tape recordings on the past year's work are now in hand for the following species of *Uca*: *dussumieri* (Milne-Edwards), *coarctata* (Milne-Edwards), *tetragonon* (Herbst), *vocans* (Linnaeus), *maracoani* (Latreille), *vocatur* (Herbst), *rapax* (Smith), *thayeri* Rathbun, *lactea* (de Haan) and *cumulanta* Crane. Some of these recordings were played at the Symposium. Oscillographs are being made for inclusion in a forthcoming book on *Uca*.

It need hardly be stressed that the work on acoustics in the genus is in its infancy. For a history of the study to date refer to Salmon (1965).

C. *Displacement activities*

Displacement behaviour plays such an important role in the ritualization of *Uca* display that several paragraphs will help make the following section clear. Displacement behaviour is defined in this context as the release of energy, accumulated through the frustration of one or more drives, by activity characteristics of another drive. No attempt will be made to distinguish between displacement behaviour and redirected activities. In fiddler crabs the displacement or redirection is often, in single individuals within a few seconds, so rapidly changed and so often only partly ritualized, that it seems best to keep terminology to a useful minimum.

Fiddler crabs, depending on species and circumstances, often make feeding and cleaning motions in the middle of display. They also, it is now clear, stridulate or rap the ground with the cheliped when the occasion does not normally elicit this response.

These motions, often incomplete and ineffective, may be either true displacement behaviour or ritualization, as will be indicated below.

Displacement behaviour in *Uca* was first reported by Gordon (1955), who described incomplete feeding behaviour in a species in South Africa. I have seen it repeatedly in every species in which advanced visual display is familiar to me. It is of questionable occurrence in the socially least advanced species in the Indo-Pacific, a group in which visual display is least developed. In contrast it is exceptionally prevalent in species in which display and territoriality reach their height.

D. *Annotated list of the principal elements in* Uca *display and their apparent origins*

(1) *Major cheliped*

(*a*) *Visual signal.* Vertical wave, the flexed cheliped moving up and down in a single plane in front of body. Forms entire visual courtship display in some Indo-Pacific species. Apparent origin: ritualized displacement feeding (figure 4*A*, *B*). In some species perhaps derived directly from acoustic signal (*f*), below.

(*b*) *Visual signal.* Vertical wave, as in (*a*) above, but with jerks. Found in various parts of the genus in threat and courtship. Examples: *rosea* (Tweedie), *mordax* (Smith). It is clearly a development of (*a*) above, each upward jerk representing a single wave, started at a level where the preceding wave reached its peak, without descent.

(*c*) *Visual signal.* Cheliped partly unflexed during wave, pushing out to an acute angle with the front. Example: *chlorophthalmus* (Milne-Edwards). A development of (*a*) or (*b*), with the jerks largely smoothed out.

(*d*) *Visual signal.* Lateral wave, the cheliped being unflexed outward and either returned to rest position in a single plane (example: *speciosa* (Ives)), or carried on up, around and down in a circular motion (example: *lactea* (de Haan)). Apparent origin: ritualized lateral threat posture (figure 4*C*, *D*).

(*e*) *Acoustic signal.* Vibration of flexed cheliped against side of burrow. A warning signal in burrow against intruder widely distributed in genus. Sometimes also a regular part of courtship display (example: *cumulanta* Crane). Sometimes widely used in courtship at night (examples: *tangeri* (Eydoux), *pugilator* (Bosc), all through the work of Altevogt, von Hagen, Salmon & Stout and Salmon in *loc. cit.*). Apparent origin: ritualized displacement feeding.

(*f*) *Acoustic signal.* Vibration of flexed (or, rarely, unflexed) cheliped against substrate beside or near burrow mouth. Surface equivalent of (*e*), of which it is a development. Examples: same as above.

(*g*) *Visual signal.* Ritualization of (*f*). Shown when the vibration does not reach the substrate, it is most surely detectable in motion picture close-ups with the camera on or near the ground. In some species, where it does not occur as a regular part of display, the action doubtless represents displacement vibration. Both (*f*) and (*g*) often occur in the same individual (examples: *deichmanni* Rathbun, *saltitanta* Crane) during moderate to high intensity display, both in threat and courtship.

(*h*) *Acoustic signal.* Vibration of major merus against outer suborbital margin or its vicinity. Occurs during high intensity threat display. Example: *vocans* (Linnaeus). Rare on surface, probably common underground, judging by prevalence of appropriate morphological specializations. Apparent origin: ritualized displacement cleaning.

(2) *Minor cheliped*

(*a*) *Visual signal.* Incomplete feeding motion. Occurs during high intensity display, both threat and courtship. Characterized by rapid shaking of the small claw which is sometimes contrastingly lightened or coloured. Examples: *festae* Nobili; *lactea* (de Haan) in Taiwan. Sometimes not distinguishable from (*b*) below. Apparent origin: ritualized displacement feeding.

(*b*) *Acoustic signal, visual signal or both.* Minor merus vibrated against suborbital region or its vicinity, or in the air in front of it. Occurs during high intensity display, both threat and courtship. Example: *limicola* Crane. Apparent origin: stridulation or ritualized stridulation, probably originally derived, like 1(*a*) from displacement feeding.

(*c*) *Visual signal.* Cleaning motion of claw, directed toward manus or chela of major cheliped. Occurs during high intensity display, both threat and courtship. Example: *oerstedi* Rathbun. Apparent origin: displacement claw-cleaning, probably never fully ritualized.

(*d*) *Probably a tactile signal.* Plucking at female carapace, often combined with incomplete feeding motions from mud-covered patches of pile. Actual feeding from the clinging mud and, possibly, associated algae seems to occur in some species. Typical of pre-copulatory behaviour. Apparent origin: ritualized feeding. Sometimes the motion, perhaps with another origin, consists only of patting or stroking, instead of plucking.

(3) *Ambulatories*

(*a*) *Acoustic signal*. The meri of one or more adjacent walking legs, on either or both sides, are rubbed together. The motion occurs in both sexes, and in all parts of the genus, although apparently not in all species. Morphological specializations consist of serrations on the upper margins of the segments and series of tuberculated striae on the posterior surfaces (figure 5*A*, *B*). A high intensity threat signal, it is frequently seen on the surface and strongly suspected to be the mechanism of many of the sounds made underground. Example of surface signals: *dussumieri* (Milne-Edwards). Apparent origin: ritualization of displacement cleaning motions.

(*b*) *Visual signal*. Motions similar to those in (*a*), but the meri do not touch, and the legs are often raised rhythmically very high in the air during single waves. Occurs in the male only, and only during high intensity display, in both threat and courtship. Examples: *demani* Ortmann; *rapax* (Smith). Apparent origin: ritualization of stridulation by walking legs described in (*a*).

(*c*) Visual signal. Walking legs momentarily depressed, so that the crab repeatedly bobs up and down in a 'curtsy'. Characteristic of high intensity courtship. Widely distributed through the genus in socially advanced species. Example: *lactea* (de Haan). Apparent origin: an intention movement, with display and burrow descent tendencies in conflict.

(4) *Efferent branchial apertures* (anterior buccal region).

(*a*) *Acoustic signal*. 'Bubbling' through emission of bubbles connected with respiration (figure 5*C*). Warning signal against intruders, both sexes, normally taking place in burrow. This sound is frequently heard in many species. At first it was considered a result of normal respiration. It is now believed to be fully under the control of the crab and to be a signal widely used against intruders. Example: *tetragonon* (Herbst). Apparent origin: ritualization of part of the respiratory process.

(5) *Membranes at bases of chelipeds*

(*a*) *Acoustic signal*. Vibration of membranes, apparently by means of air and water circulating through adjacent respiratory system. Morphological specializations include species-specific patterns of striation visible on membrane in living crabs, at least at base of minor cheliped. The sounds normally serve as warning signals against intruders in the burrow, but have also been produced when the crabs are held in the hand and observed under a dissecting microscope. Example: *vocatur* (Herbst). Apparent origin: ritualization of part of respiratory process (figure 5*C*).

E. *Incomplete ritualizations*

Often it is impossible for the observer to be certain, even in the study of motion picture close-ups, whether at a given moment a movement made by a displaying individual is fully ritualized in the fashion characteristic of the species, or is serving as a displacement activity, or is functioning in its evolutionarily original capacity. Particularly in an element such as no. 3 (*b*), above, with its apparent history of two ritualizations, uncertainties are frequent. It may remain unclear whether a given crab is cleaning its walking legs, stridulating or performing visual signals, highly ritualized and altogether soundless.

In conflict situations, species with highly evolved display patterns often mix in display an impressive number of additional motions. An example was shown in the film presented at the Symposium. A male *lactea* in Singapore was courting a female intensively. In this species display consists basically of a circular lateral wave (no. 1(*d*)) at the rate of less than one to the second, along with rhythmic elevations ('kicks') of the walking legs (no. 3 (*b*)), accompanied, at a female's approach, by a fast repeated bending of the legs in a 'curtsy' (no. 3 (*c*)). Disturbed either by a neighbouring male or by the proximity of the camera, the displaying crab added the following elements, while continuing his regular display: he performed incomplete feeding motions, the minor cheliped neither bringing up substrate nor actually touching the buccal area; he made ineffective motions toward the immaculate major cheliped, as though in cleaning; finally the second and third walking legs, on the right side only, were rubbed together during their elevation, in apparent stridulation, while the usual separate kicks continued on the left. (A sound tape was later recorded in Fiji under similar conditions, proving that threat stridulation by this means takes place in the species.) Finally, the Singapore individual extended the major cheliped forward, stopped waving, and vibrated the tips of the claw up and down without apparently touching the substrate (no. 1 (*g*)), in a sometimes omitted facet of high intensity courtship.

6. CONCLUSIONS

A principal result of this study is the evidence of parallelisms with vertebrates in the evolution of social behaviour in fiddler crabs. As in numerous fish, birds and mammals, aggressive tendencies are ritualized through both morphological specializations and through activity sequences, preventing serious injury. These characteristics apparently also reduce the frequency of delays in breeding that sometimes follow defeat.

As in many other animals the origins of display are often clearly traceable to changes of form and function in such basic activities as feeding and cleaning, as well as through the incorporation of elements from patterns of aggression.

A great deal of work is now needed to put many of these observations on quantitative and experimental bases. For example, fights, although of uncommon occurrence in the field, can fruitfully be scored for intensities and results. Means must first be worked out for keeping marked individuals under observation in their natural habitats, in spite of their wandering phases.

Invertebrates have been largely neglected by ethologists. Reese (1964) in his helpful ethological review of crustaceans, indicates the possible scope of work in that single small group. The present study of fiddler crabs gives, it is hoped, an idea of the size of their behavioural repertories and the evolutionary interest of their apparent ritualizations. Similar work on other invertebrates should yield comparisons of interest to students of social behaviour in both animals and man.

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