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ACOUSTIC 'CALLING' BY FIDDLER AND GHOST CRABS

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SUMMARY

Male fiddler and ghost crabs are unique among the Crustacea in their use of acoustical signals to call females during the breeding season. This paper reviews what has been learned about the sound-producing mechanisms, signal characteristics, calling range, detection abilities and the behavioural responses of the crabs to the calls. Evidence is also presented to suggest that species differences in call structure are heritable.

Recent studies indicate that differences in calling behaviour in the two groups can be related to burrow zonation and access to water, and are best conceived as representing a continuum of change rather than two (or more) distinct patterns. Finally, directions of future research are outlined which emphasise where needed experimental studies would be most appropriate.

I. INTRODUCTION

It has been about thirty years since the importance of nocturnal sound production in the courtship of fiddler and ghost crabs became apparent. I do not mean to imply that nothing was known beforehand. On the contrary, a number of earlier, largely anecdotal accounts by naturalists documented the occurrence of ghost crab 'choruses', heard on quiet tropical nights by keen listeners. Anatomical studies revealed the well-developed stridulatory and 'tympanal' organs of ghost crabs and their relatives. But the widespread use of sound among these animals and its role in communication were matters for speculation. Indeed, virtually nothing was known about hearing in terrestrial crabs, whether sounds were produced by one or both sexes, or how the crabs themselves responded to the acoustic stimuli emitted by conspecifics. The answers had to await the development of suitable tape recorders, transducers, and speakers, none of which were available until the 1950's.

Many of these questions can now be partly answered; others still remain. My purpose in this paper is to summarise the present state of our knowledge, emphasising where the gaps have been filled and where they still remain. I will also indulge in some speculation which I hope may form the basis for hypothesis-testing by future workers. I shall not attempt to cite the historically pertinent literature, as most of this is referred to in my earlier reports, those of my collaborators, or reviews (Schöne, 1968; Salmon and Atsides, 1968; Horch, 1971, 1975; Crane, 1975; Weygoldt, 1977). Rather, this paper will emphasise significant contributions over the last 20 years.

Before proceeding, a few words are necessary to place this particular topic in its biological perspective. The use of sound as a *calling* signal is a rare phenomenon among the Crustacea. It is unknown among the marine forms. Acoustic *calling* (spontaneous sound production by a single crab, usually male) occurs only in the subfamily Ocypodinae, though other Ocypodids, as well as terrestrial crabs (Gecarcinidae, Grapsidae), use sound during *courtship* interactions (i.e. when one crab, usually a male, has detected the presence of another, usually a female). Why these differences exist is a puzzle requiring more detailed study of the groups involved. In any event, the rarity of this behavioural adaptation invites comparison between acoustic calling in the Crustacea, with their unique marine heritage, and analogous systems in terrestrial forms such as insects and frogs. Are similar mechanisms involved in the coding of species-typical information within calls? What sort of adaptations minimise the effects of noise? How are sound sources localised? What types of central processes underlie decoding and recognition? Are stimuli detected as air- or substrate-borne signals? This is not a complete list of questions, but it emphasises the rationale behind these studies. We hoped through an analysis of acoustic calling in *Uca* and *Ocypode* to

simultaneously contribute toward an understanding of their specific adaptations, and also of the general features common to calling systems in a variety of animals.

II. SIGNAL PRODUCTION, TRANSMISSION AND DETECTION

Acoustic calling by fiddler and ghost crabs is only performed by males in possession of special 'mating' burrows. The burrows are distinguished from those of non-calling males by their location and/or their structure (Linsenmaier, 1967; Lighter, 1974; Christy 1980). Calling also is most prevalent for a few days twice each month (a semi-lunar rhythm), though the exact timing with reference to lunar phase varies with species. In fiddler crabs (Christy, 1978) calling activity coincides with the timing of ovarian ripening of females. The driving force for timing display activity in males is thought to be this ovarian cycle in females. But the significance of the female rhythm itself is not understood. Zucker (1978) and Christy (1978) have hypothesised that females synchronise reproduction so as to release their larvae during optimal tides some days later. However, these authors disagree on whether tidal flow optimises larval dispersion, or prevents the larvae from being scattered too far from protected shorelines.

Fiddler crabs call by 'rapping' or by 'honking', depending upon species (Fig. 1). Rapping species rapidly 'vibrate' their major cheliped against the substrate. The sounds are composed of a series of pulses, each of which represents one strike between the base of the claw and the substratum. Species differ in such temporal features as the number and regularity of the pulses within each sound, the pulse repetition rate, the duration of each sound, and the interval between consecutive sounds.

Honking sounds are also composed of pulses, but each pulse is many times longer than the brief, plosive strikes typical of rapping species. The physical structure of the pulse is complex. It consists of harmonically related, low frequency (150-800 Hz) sounds, not unlike a brief buzz of a flying insect. In some species, the harmonics are intermingled with 1-4 brief higher-frequency pulses. The former are correlated with rapid up-and-down movements of some of the walking legs, held off the substrate; the latter, with rapid taps of individual legs against the substrate. These may not be the only structure involved in generating honking calls. Von Hagen (1975) believes that the major chela also contributes. However, I have not seen this structure move while males make honking calls. The matter will only be resolved through experiment. Honking species differ not only in the temporal patterning of their sounds, but also in the spectral energy distribution of the honk.

Calling male fiddler crabs make their sounds just outside the entrance of their mating burrows, where the movements involved can be observed. In contrast, ghost crabs call from well within the burrow so that designation of the method employed in signal production is based upon sonic structure. *Ocypode quadrata*, *O. ceratophthalmus*, and *O. pallidula* (= *O. laevis*) are designated as 'rappers' on this basis, but whether one claw or both are involved in calling is unknown. In *O. pallidula* and *O. ceratophthalmus*, there is also a lower-amplitude stridulatory component which occurs before the first pulse (Fig. 1). The rasp sounds of *O. cordimana* appear as 'pure' stridulations. Yet this species is the only ghost crab lacking a stridulatory ridge (Horch, 1975)! Regardless of the proposed mechanism for call production, each ghost crab species has a unique temporal pattern of pulses.

How are the sounds detected? Horch (1971) showed that the receptor in *Ocypode* was Barth's myochordotonal organ (MCO). Parallel studies by Salmon, Horch and Hyatt (1977) demonstrated the same receptor was used by the fiddler crabs *Uca pugilator* and *U. minax*. In both genera, the receptor is located on the merus of each walking leg. Externally, it is marked by a thin-walled 'window' or 'tympanum'. When this structure is destroyed acoustic sensitivity of the operated walking leg is reduced by up to 20 dB, especially at the higher range of frequencies the crabs can detect. At frequencies below about 300 Hz, Barth's organ is only slightly more sensitive, at least to vibrations, than other sensory units which are stimulated (probably joint proprioceptors). Barth's organ operates, then, to increase sensitivity to a higher range of frequencies than can be detected by other sensory systems. The significance of this adaptation will be discussed shortly.

An important issue centred upon whether the crabs responded to substrate or air-borne sound. In our laboratory experiments we recorded sensory input from acoustic interneurons in the supraoesophageal ganglion when stimuli were presented either through a vibrating platform or a speaker located some distance away. These tests indicated that both genera could respond to sufficient amplitudes of either sound or vibration. This was especially the case in *Ocypode*, which was somewhat more sensitive to all acoustic stimuli. Thus to resolve the question we had to measure the actual amplitudes of sound and vibration generated by the animals under natural conditions.

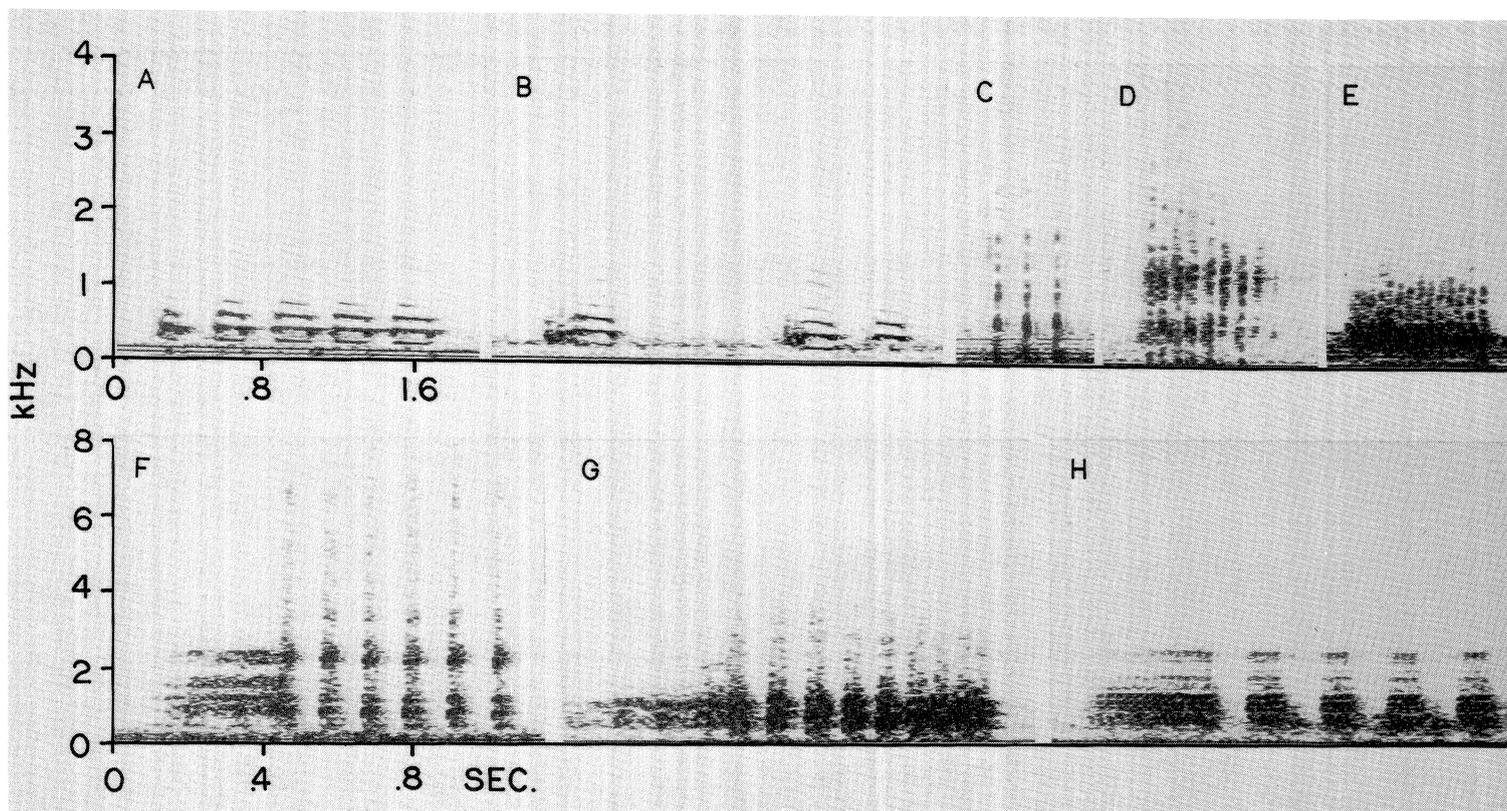


Fig. 1. Spectrograms of calling sounds produced by fiddler and ghost crabs. **A**, a honking sound of *Uca rapax*. **B**, two honking sounds of *U. pugnax*. The first consists of one pulse, the second of two. **C-E**, rapping sounds of *U. speciosa*, *U. spinicarpa*, and *U. panacea*, respectively. The pulse repetition rate for these species ranges from average values of 5 Hz (*U. speciosa*) to 23 Hz (*U. panacea*). **F-G**, rapping sounds of *Ocypode ceratophthalmus* and *O. pallidula*. Note that first rap is preceded by a lower amplitude component, probably stridulatory. **H**, rasping sound of *O. cordimana*.

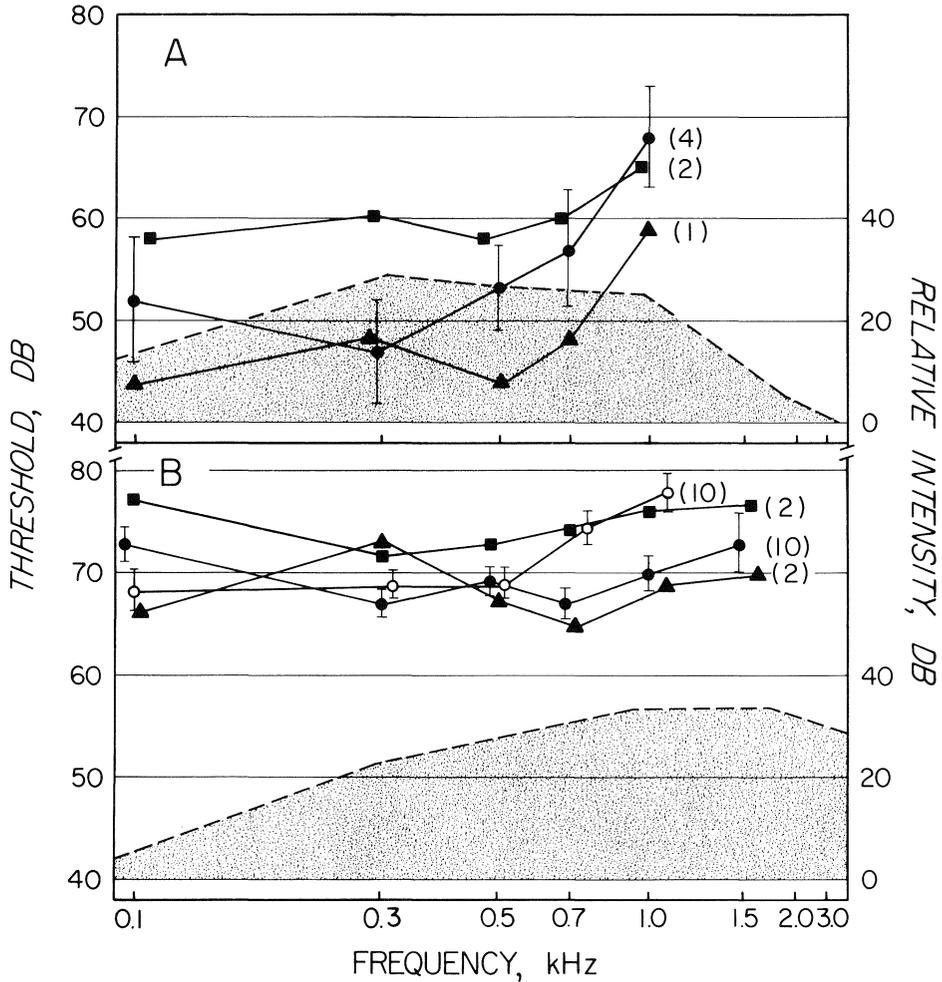


Fig. 2. Spectral energy distributions (shaded) of the sounds of *Uca minax* (A) and *U. pugilator* (B), plotted relative to background levels in the field (right scale). Superimposed on the area are thresholds (mean \pm SE) for acoustic interneurons to pure tones in dB re: 10^{-3} cm/sec² (left scale). Values in parentheses indicate number of cells in the sample, O, \bullet , tonic cells; \blacktriangle , inhibited cells; \blacksquare , phasic cells. From Salmon and Horch, 1976.

These measurements indicated that only on the quietest nights were the air-borne components of the calls above background and even then, scarcely so. When noise from such sources as wave action or wind completely masked the air-borne component, males continued to call. On the other hand, the substrate proved to be amazingly noise-free, even on windy nights. Horch and Salmon (1971) found that the relatively loud sounds of *O. ceratophthalmus* existed at suprathreshold amplitudes 8-10 metres away from calling males, when measured as vibration. For the smaller fiddler crabs, the calling distance was much less; 50-100 cm (Salmon and Horch, 1972). These results suggested that the biologically significant channel was substrate vibration.

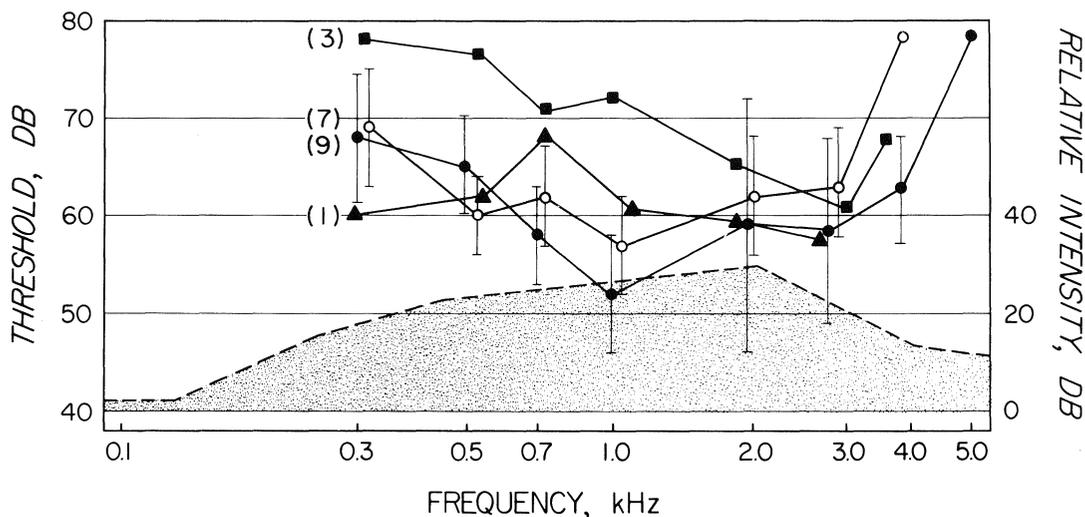


Fig. 3. Spectral energy distribution (shaded) of rapping sounds of *Ocypode quadrata*, plotted in conjunction with thresholds of its acoustic interneurons. Format as in Fig. 2. From Salmon and Horch, 1976.

Horch (1975) also found that the substrate had two additional properties which heightened its utility as a communicatory channel. First, when the substrate was damp, vibrations attenuated much more slowly than when it was dry. This finding suggested why all male ghost crabs called from lower regions of the supralittoral zone where the substrate was moist. Secondly, he found that the velocity of substrate-borne vibration was slower than air-borne sound (200 m/s vs. 350 m/s). Arrival time cues therefore may be important in localising vibration sources. For fiddler crabs, legs nearest a source of vibration would be stimulated about 0.25 ms before those farthest; in the larger ghost crabs, the difference would be about 0.5 ms. These values are well within the range of resolution by other arthropods such as scorpions which locate prey by vibrational cues (Brownell and Farley, 1979).

In calling systems of other animals there is a matching between the sensitivity of the receptors and the spectral energy distribution of the sounds produced during communication. We were therefore anxious to determine if similar relationships existed in the fiddler and ghost crabs. Figures 2 and 3 show spectral sensitivities for three representative species: *Ocypode quadrata* and *Uca pugilator* (rappers) and *U. minax*, a honking species. For the two rappers, vibration sensitivity was more restricted in range than the spectral energy composition of the sounds. However, the high-frequency components of rapping sounds attenuate rapidly and, at near-threshold distances, are not present. Thus, the tuning curves are centred upon the lower frequencies that are most useful for distance communication. The situation for *U. minax* was different. Here, the sensitivity curve more closely matched the spectral composition of the sounds near the calling male. In this species, however, sounds were produced by males only when they detected the movements of another crab nearby; thus attenuation effects were of little consequence.

The significance of Barth's MCO may be appreciated by considering signal-to-noise conditions under which the crabs must detect vibration. The substrate is a relatively noise-free environment compared to the sound channel in air, but noise is still present. It is confined to the very low frequencies (500 Hz and below). If the crabs were to depend upon joint proprioceptors for detecting signals, they would by necessity have to produce signals which fell within this band of noise. Barth's MCO, by extending the range of frequencies upward, allows the crabs to signal and detect just above this band of noise, where frequency-dependent attenuation effects are minimised. In the ghost crabs, which have the largest calling range, sensitivity below 500 Hz is poor. This adaptation should actually improve detection by excluding competing noise, thus improving the signal-to-noise ratio.

III. INFORMATION CONTENT AND BEHAVIOURAL RESPONSE

It is one thing to note correlations between male calling and female reproductive cycles, call structure and species, or sound production and exquisite abilities to detect these signals. It is quite another to

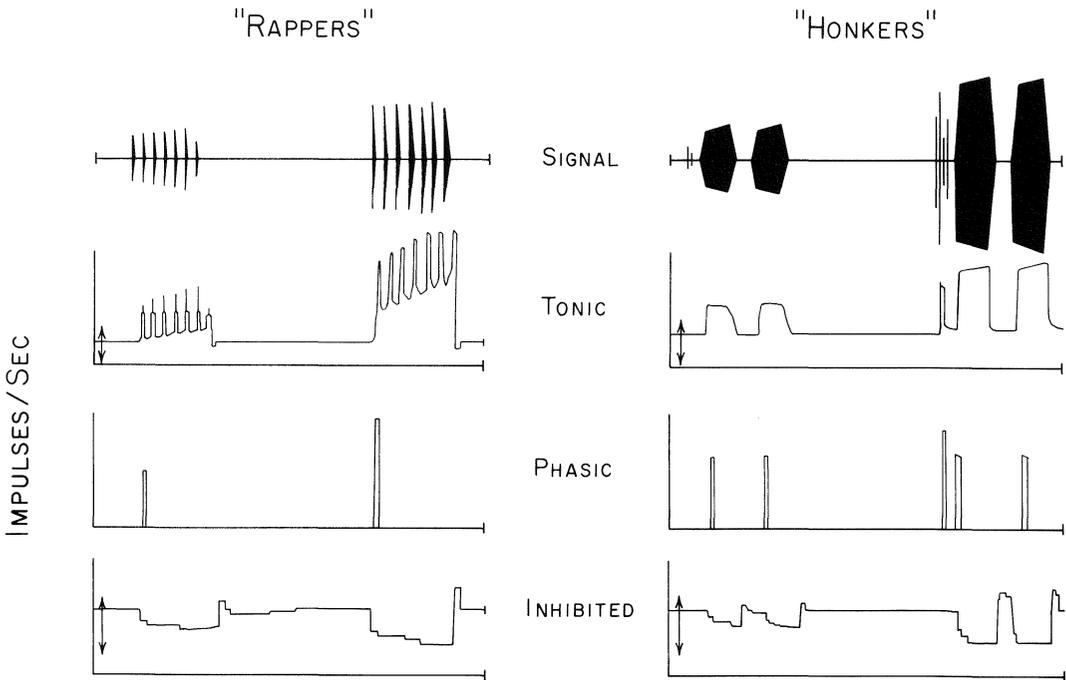


Fig. 4. Responses of tonic, phasic and inhibited units to rapping and honking sounds (signal) of two amplitudes. Data based upon presentations of signals to preparations under laboratory conditions. Tonic cells code pulse number; phasic cells, sound onset; and inhibited cells, sound duration. All cells show stronger responses to louder signals. Vertical, double-pointed arrow indicates cell shows variable rate of spontaneous firing.

prove that the crabs respond to the calls or can appreciate call differences. Sound lends itself nicely to experiments testing these features, since it can be presented as a playback either to crabs in the field or to preparations, while excluding other parameters of calling males such as their associated visual or chemical cues. In this section I will review our electrophysiological studies which indicate how the crabs process features of the sounds. Then I will summarise field data from experiments with males which show how they respond to one another's calls.

A. Electrophysiological experiments

Barth's MCO is innervated by clusters of two cell types which differ in size. These send axons into the leg nerve which enters the thoracic ganglion. In our initial experiments (Salmon and Horch, 1973) done with *U. minax*, we recorded from preparations eviscerated to expose the thoracic ganglion and the proximal portion of the leg nerves. When electrodes were inserted into the nerve, two classes of units were found: tonic and phasic. The former responded to vibrational stimuli with a continuous burst of impulses. The latter were at least 10 dB less sensitive and responded with many fewer impulses of much greater impulse amplitude. Both types of units continued to respond when walking leg segments distal to the merus were removed. However, the response was abolished when ablation included the merus. Latencies for these fibres were typically 3–5 ms.

Eviscerated preparations, while allowing us to identify the properties of sensory units, were of limited utility because we could not keep the animals alive. Thus thresholds we obtained were abnormally high, probably because the walking legs were resting limply upon the testing surface used to present vibrations. It proved rather simple to make a small hole in the exoskeleton just above the mouthparts to expose the supraoesophageal ganglion and record from acoustic interneurons located there or in the connectives. The crabs were relatively unaffected by this operation and remained vigorous during the recordings. Not only were thresholds much lower, but the units themselves proved especially interesting, responding to different features of the sounds. We used *U. minax*, *U. pugilator*, and *O. quadrata* as subjects. All three species possessed the same types of units: tonic, phasic, and inhibited (Salmon and Horch, 1976).

Tonic cells were similar to those found at the sensory level. They responded with a burst of impulses throughout the course of stimulation. They differed from sensory units by showing varying amounts of spontaneous firing. Inhibited units were spontaneously active prior to stimulation. This activity was decreased during stimulation, the amount depending upon stimulus amplitude. Phasic units responded with a single impulse to a vibrational stimulus, provided it occurred with a rapid onset. After firing they required at least a second to recover. None of the units coded tonal frequency; that is, it was impossible to distinguish between responses to 400 Hz from those of 700 Hz or 1 kHz. However, the units were tuned to respond best to certain frequencies, typically those most prevalent in the species' sounds (Figs 2 and 3).

Figure 4 summarises the responses of the units to stimulation by natural sounds and shows the manner in which temporal features of the calls are coded at low (i.e., some distance from the male) as well as higher stimulus levels. It is clear that most of the significant temporal properties of the calls are resolved.

Several other features of these neurones should be mentioned. First, all the cells were non-habituating. By this, we mean they continued to respond to consecutive presentations of crab sounds (or pure tones), delivered at biologically appropriate rates. Secondly, in their non-habituation, as well as their particular response characteristics, they were remarkably similar to the pulse- and chirp-coding neurones found in female crickets by Stout and Huber (1972). We therefore consider the crab interneurones to be vibration-sensitive analogues of the cricket cells. Thirdly, the cells were non-specific in the sense that those of one species responded to the calls of the other species we tested. Thus, these interneurones are not those used in making discriminations, though they probably supply information to the cells that do. Lastly, all the interneurones ceased to respond to acoustic input when the animals moved (began walking). During locomotion, therefore, input is somehow blocked. No doubt this is a form of 'overload protection', since during walking Barth's MCO is subjected to mechanical stimulation many times more powerful than that associated with the calls. This finding suggests that the crabs can detect calls only during pauses in movement, and that vibrational orientation must involve successive temporal comparisons interspersed between movements toward or away from the source. One can only wonder if overload protection also operated within the nervous system of calling males to shield them from their own sounds.

B. Behavioural responses

The majority of crustaceans pair briefly. The sexes then separate and females brood their eggs until they hatch. The larvae enter the plankton. These facts bias most crustaceans toward polygynous mating systems, in which males are most successful if they outcompete other males for access to females, and females enhance their reproductive success by selecting the 'best' males. The criteria used by female ghost crabs in mate selection are unknown. In the fiddler crabs *U. rapax* and *U. pugilator*, the largest males seemed to be preferred (Greenspan, 1975; Hyatt, 1977). However, for *U. pugilator*, Christy (1980) found this to be an oversimplification. Females preferred to mate with males possessing mating burrows above the intertidal because these burrows did not collapse at high tide. Christy found that after mating, females remained within a side branch of the male's burrow where they extruded and incubated their eggs. It took several days for newly extruded eggs to become firmly attached to the female's pleopods. If the burrow collapsed, most of the eggs were lost during this critical stage. In crowded colonies, males competed aggressively for access to high beach areas and only the largest were successful in obtaining and holding burrows there. However, if a smaller male could hold a high beach burrow, he was selected by a female as often as a larger male.

Competitive interactions between males are not confined to the daylight hours. Acoustic interactions occur during nocturnal periods which are analogous to similar phenomena in insect (Alexander, 1975) and anuran (Wells, 1977) choruses. Natural selection should favour a male who can alter his signalling behaviour so as to minimise the effects of competitors. Doing so makes his own signal more conspicuous and might coax a female away from a neighbouring male and toward him. A number of these responses have been documented in ghost and fiddler crabs, and some have been experimentally induced through playback experiments. The responses fall into the following categories:

(1) **Induced calling responses.** Male crabs of both genera call in bouts lasting several minutes. They pause to feed, modify their burrows, or perhaps rest. Should a neighbouring male within acoustic detection range begin calling more vigorously, the temporarily silent male will often join in. Presumably, the neighbour's behaviour indicates a female is nearby. The response of the silent male increases his probability of attracting her too. Since females usually visit several males before making a final selection, this response

is obviously adaptive. Salmon (1965) demonstrated this response somewhat indirectly. He frightened calling males (*U. pugilator*) into their burrows, then timed their return to the surface and subsequent calling with and without a playback of another crab's sounds. Those males receiving the playback began calling significantly sooner.

(2) **Changes in calling 'vigour'**. Neighbouring groups of calling males will often increase their rate and amplitude of sound production for a few seconds, then return to a previous lower 'spontaneous' rate. These changes only involve males which can detect one another's calls. In fiddler crabs (and presumably ghost crabs), such shifts are initiated by one male which has been stimulated either by nearby walking movements of another crab or by actual contact between a wanderer and the caller. Salmon (1965) did playback tests in which calling males were presented with sounds of a single male that varied in tempo, from the usual (16 sounds/min) to the calling rate of stimulated individuals (24/min). Only the latter induced tested males to significantly increase their calling rate over the pre-playback level. After the playback (which lasted one minute), the test male quickly returned to his ambient rate of calling.

(3) **Avoidance of call overlap**. Horch (Horch and Salmon, 1971; Horch, 1975) has documented changes in the inter-call intervals by neighbouring ghost crabs that result in avoidance of call overlap. Playback tests were used to show that the changes in a male's behaviour are deliberate, i.e. that overlap was avoided significantly more often than predicted by chance. These responses occur not only within species, but also in mixed species assemblages (*O. ceratophthalmus* and *O. cordimana* in Enewetok, Marshall Islands; *O. ceratophthalmus* and *O. pallidula* in Hawaii).

Overlap avoidance probably has several advantages. First, and most obviously, a male that avoids overlap between his calls and those of a conspecific presents a distinct signal, most easily evaluated by a prospecting female. But this explanation does not account for responses to heterospecifics, as males of another species are not reproductive competitors. Though each species of ghost crab produces sounds with a distinctly different temporal pattern, all calls have been shaped by natural selection to maximise transmission range. This is accomplished by concentrating most of the spectral energy of the call in the lowest frequencies just above background (500 Hz–3 kHz). For this reason, the sounds of all three species of ghost crabs are remarkably similar in their spectral energy distribution (Fig. 1), and thus constitute a masking noise for one another. Interspecific call avoidance responses preclude such masking effects.

It is curious that overlap avoidance does not occur in North American fiddler crabs. One possible reason is the much closer spatial proximity of calling males which may result in acoustic contact between too many neighbours for a call avoidance response to evolve.

IV. EVOLUTION OF ACOUSTIC DISPLAY

It has been largely assumed that the particular characteristics of each species' calling display are heritable, and therefore shaped by natural selection. However, the relationships between genome and behaviour within the Crustacea are virtually unknown. Selection experiments have never been done. Behavioural analyses of hybrids and their backcrosses, comparable to the work of Bentley and Hoy (1972), were until recently limited to non-calling species (e.g. Solignac, 1976).

In this section I will review recent work which provides some insight into heritable components of acoustic display, as well as an example of microevolutionary changes in call structure. Then, I will critically evaluate some old hypotheses and present some new ones which seek to explain how basic patterns of display in fiddler and ghost crabs might have evolved.

A. Reproductive isolating mechanisms in *Uca*

Uca pugilator was once believed to be a single species extending from Massachusetts to Florida on the Atlantic coast and from Florida into Mexico along the Gulf coast. However, field studies showed that in northern Florida it was replaced by a structurally similar species (*U. panacea*) which is the most ubiquitous form west of Florida. The two species overlap from Cedar Key to Pensacola, Florida. The distribution of *U. pugilator* west of Florida is unknown, except that it is rare.

While the two species are difficult to separate on the basis of morphology, they are easily distinguished by their premating displays. The rapping sounds of *U. panacea* contain over twice as many pulses, produced at about twice the rate (Fig. 5). The waving displays of the two forms are similar, though they can be separated on the basis of subtle differences in form and emphasis (Salmon *et al.*, 1978).

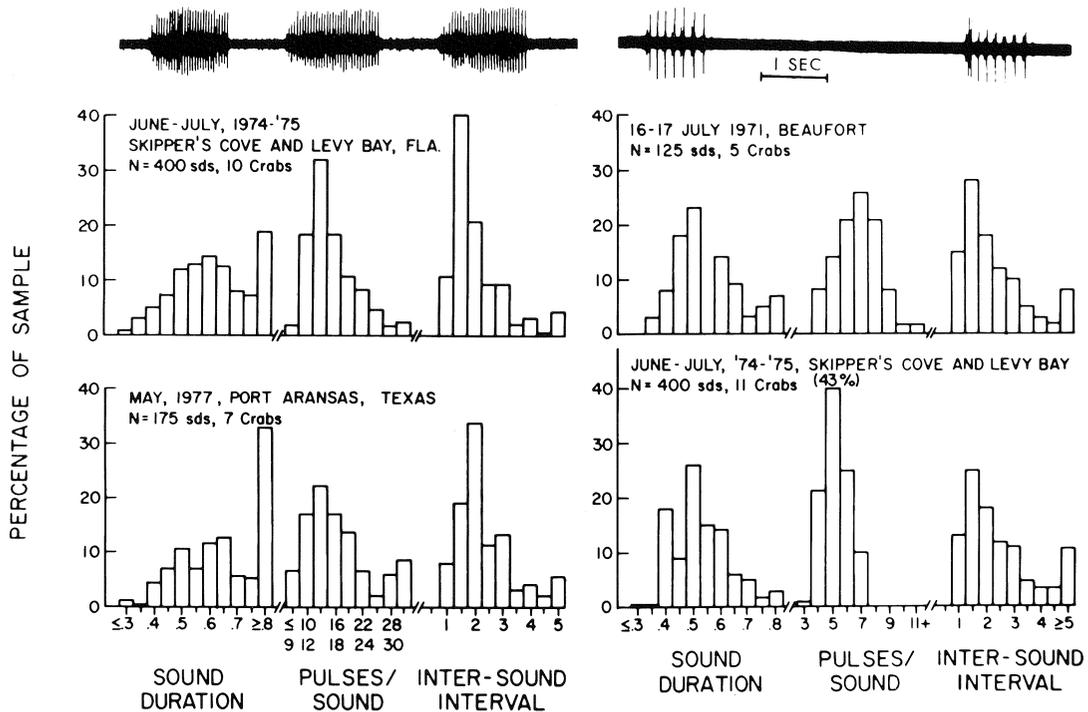


Fig. 5. Temporal properties of rapping sounds produced by *Uca panacea* (left) and *U. pugilator* (right). The pulse repetition rate for the former averages about 23 Hz throughout its range. For the latter, it is 12 Hz in Beaufort, N.C., where *U. panacea* does not occur; it averages 9.5 Hz at Skipper's Cove and Levy Bay, Florida, where *U. panacea* is sympatric. Note also that the number of pulses per sound is reduced in the overlap zone. See text for further details. Modified from Salmon *et al.*, 1978.

I believe that the two species diverged from common stock and then came in contact before they were capable of avoiding interbreeding. Evidence in support of this hypothesis comes from an analysis of their call structure. Male *U. pugilator* from North Carolina produce sounds with an average pulse repetition rate of 12 Hz, but when they are sexually stimulated, the rate may go as high as 17-18 Hz. The latter falls close to the lower range of variation shown by male *U. panacea* (21 Hz). A comparison between the calls of *U. pugilator* in the overlap zone and those in North Carolina indicated significant change. The former called at a reduced pulse repetition rate (mean of 9.5 Hz) and their sounds were composed of fewer pulses. Both changes made their calls more distinct from those of *U. panacea*.

I presume that selection by females has been the driving force altering the call structure of conspecific males in Florida. But what are the penalties against indiscriminate females? Hybrids have not been found in nature, but under laboratory conditions males occasionally succeeded in forcing interspecific copulations. The offspring suffered higher mortality through the developmental stages and as adults were sterile (Salmon and Hyatt, 1979).

The call structure of the hybrids is shown in Fig. 6. We (Salmon and Hyatt, 1979) found that the pulse repetition rate was intermediate between the two parental forms. Note that there are also distinct differences between the reciprocal crosses in sound duration as well as the number of pulses/sound. These data strongly support the notion that call structure is under close genetic control.

B. Patterns of display in fiddler and ghost crabs

There is general agreement that fiddler and ghost crabs are more closely related to one another than to any other group (Crane, 1975). But they show many differences in their ecology and behaviour. In the past, their sexual behaviour patterns have been treated separately, as if few similarities existed and as if no general inferences could be drawn to relate differences along a continuum of selection

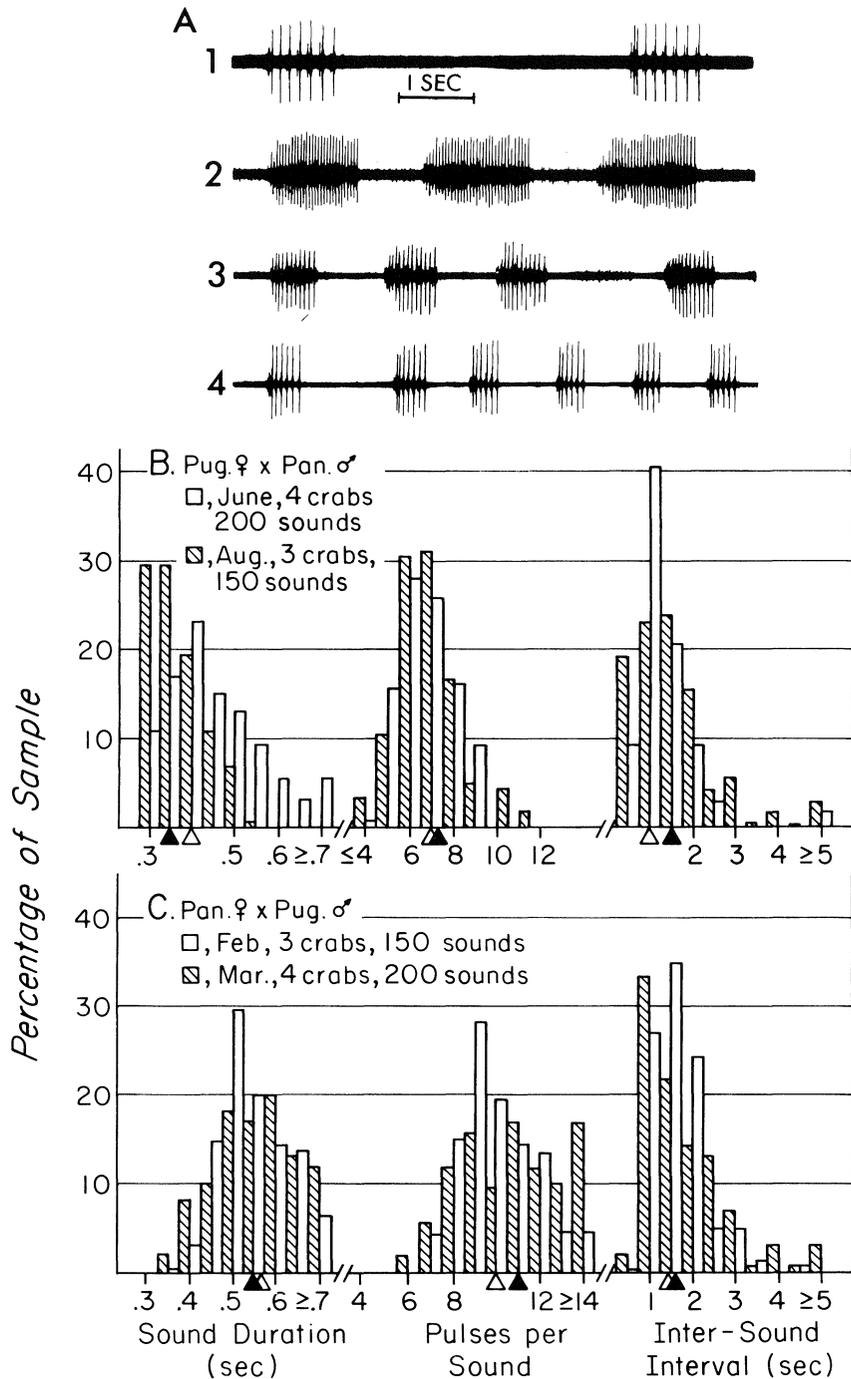


Fig. 6. Temporal properties of the calling sounds produced by hybrids between *Uca panacea* and *U. pugilator*. **A**, oscillographs of rapping signals produced by *U. pugilator* (1), *U. panacea* (2), *panacea* ♀ × *pugilator* ♂ (3), and *pugilator* ♀ × *panacea* ♂ (4) hybrids. **B**, **C**, quantitative analysis of the sound structure for each cross during the first year of development. △, ▲, median category. Modified from Salmon and Hyatt, 1979.

pressures. Enough new information has been gathered now to suggest that the two genera should be conceived of as overlapping in some features of their ecology and reproductive behaviour. In this section I will first review courtship patterns in fiddler crabs, then present evidence which supports the above claim.

(1) Courtship patterns in fiddler crabs. Based upon present information, fiddler crabs show three basic patterns of courtship display. The first of these is typical of tropical species found in the Indo-Pacific, called the 'narrow fronts' by Crane (1957). These species tend to mate on the beach surface. Sound plays no role in calling, and waving occurs only as a courtship signal. Typically a male leaves his burrow, approaches a nearby female, and waves as he moves toward her. A receptive female does not retreat, allowing the male to grasp her and manoeuvre her into a copulatory position.

The second pattern is characteristic of New World tropical species where mating takes place in the male's burrows. Waving occurs as both a calling and a courtship signal. That is, males will wave when no female is present, but in response to a wandering female, waving becomes much more vigorous. Should the female be attracted, the male precedes her into his mating burrow and begins producing sonic signals. The latter are presumed to induce the female to follow and also present additional cues for species identification.

The third pattern is found in most (but not all) of the subtropical and temperate species. It differs from the second pattern by the addition of a nocturnal phase of courtship, employing sound as a calling signal. But this adaptation is probably associated with latitude rather than species composition. For example, *U. rapax* in Trinidad shows a typical second pattern there; it courts only during the day. Florida populations, however, show nocturnal activity and acoustic calling (Salmon, 1967). At the same time, latitude is not the only factor. *Uca minax*, which occurs as far north as Massachusetts, shows strong tendencies toward nocturnal locomotor activity, but males do not call. They do, however, court with sound at night.

A major question, currently unanswered, is that of the selection pressures responsible for these different courting patterns. Crane (1957) proposed that the surface-mating species of the Indo-Pacific were most primitive, both structurally and behaviourally, while the New World forms were phylogenetically advanced. There is some question, however, whether the genus *Uca* is really a monophyletic assemblage of species (M. Türkay, pers. comm.) which can be placed on such a 'primitive' to 'advanced' continuum. One could also argue that the differences represent alternative ecological solutions. For example, Christy (1980) hypothesises that many fiddlers may exist under one of two types of ecological conditions; those in which the food supply is spatially separated from areas where mating takes place, and those where it is not. In the former, typical of many broad front *Uca* and the ghost crabs, females feed at the lower intertidal but select mates with high beach burrows. In the latter, typical of the narrow fronts, burrows are located in organically rich, muddy substrates where they rarely collapse and are also safe incubation sites. As a result, females are relatively sedentary and 'defendable'. The 'broad front' pattern, then, with its emphasis upon dramatic male display, may be an outcome of male-male competition for high beach mating burrows and the necessity of attracting undefendable females from a distance; the 'narrow front' pattern, with its surface matings and simple waves, may result because males can defend a harem of sedentary females which the males visit at intervals for the purpose of mating.

But why did the nocturnal calling phase evolve among some of the broad fronts? Some years ago I (1965) proposed that the evolution of nocturnal calling might enable some temperate populations to complete fertilisation and reproduction more rapidly in a breeding season shortened by climatic extremes. Christy (1980) criticised this hypothesis, arguing that reproductive rates were limited by how quickly females could convert food to egg clutches and implying that male behaviour could not speed the process. He is, of course, correct with regard to ultimate limits on fecundity. But, once a female is receptive, she must find a high quality mate if she is to maximise her reproductive success. Since a male who has attracted a female into his mating burrow is 'out of circulation' for at least one low tide, the supply of optimal males may in fact be limiting. But if males could return to courtship by the next low tide, *regardless if it occurred at night or during the day*, the turnover time for optimal paired males would be shortened. This adaptation would increase the reproductive success of both sexes. The net effect would be more matings of higher quality per unit time.

The matter will only be resolved when experiments are done. But until they are, I believe this explanation is at least plausible. Christy's alternative, that nocturnal activity is linked to a poorer food supply, seems inadequate to me. There is no reason to assume all northern habitats are depauperate in this regard. They may, in fact, be more productive.

(2) Display patterns in ghost crabs, and an attempt at a synthesis. There are 19 species of ghost crabs, most of which occur in the Indo-Pacific (Bliss, 1968). The group, as a whole, spans a wider range of habitats than the fiddler crabs: from the extralittoral (*O. cordimana*) to the intertidal (*O. gaudichaudi*). The few species studied in any detail also show great flexibility in their locomotor activity patterns (reviewed in Vannini, 1976) as well as display format (Linsenmaier, 1967). Thus, a more complete study of the entire genus might provide insights into the selective forces shaping not only their behaviour, but also the behaviour of their intertidal relatives. For example, do intertidal *Ocypode* show calling behaviour patterns similar to the fiddlers? How do these patterns change as species preferences become more terrestrial? To answer these questions a survey of the admittedly fragmentary information is in order.

The ghost crabs can be divided into three groups of species, differing in zonation of their burrows, activity, and reproductive behaviour. For example, *O. gaudichaudi* and *O. ryderi* occur in the intertidal to low supralittoral zones (Crane, 1941; Vannini, 1976). Both species are active during diurnal and, in some locales, nocturnal low tides. Nothing is known about the reproductive behaviour of the former, but male *O. ryderi* court females with waving signals during the day (Vannini, 1976). Both *O. ceratophthalmus* and *O. saratan* are exclusively supralittoral as adults. As a rule, neither species shows tidal rhythms of activity. Rather, adults are predominantly active at night, though diurnal activity occurs in some populations under some conditions (cloudy skies, beaches devoid of human disturbance, etc.; Fellows, 1966; Linsenmaier, 1967). Males attract females during the day with sand pyramids near their mating burrows, and at night with acoustic signals (Linsenmaier, 1967; Horch and Salmon, 1971). The most terrestrial ghost crabs, *O. cordimana* and *O. pallidula*, dig burrows in the extralittoral zones (Fellows, 1966; Rao, 1968) and are exclusively nocturnal in activity. Reproductively active males move down to the supralittoral, establish mating burrows, and call at night with acoustic signals.

Viewed from the standpoint of male behaviour, the differences between the display patterns of low supralittoral, supralittoral, and extralittoral species of ghost crabs appear very profound. However, I suggest that this approach is not the most productive, as it deals with the *consequence* of evolution and not the actual *causes* of the differences (the selection pressures themselves). As an alternative, I would argue along the following lines. First, the fiddler and ghost crabs, for unknown reasons, possess a genetic tendency to use acoustic and visual displays as both calling and/or courtship signals to a degree unparalleled by any other semiterrestrial crustaceans. Second, when and how these signals are used by males must depend upon when females can search for mates. This searching exposes females not only to predators, but also to temperature and humidity conditions more extreme than those encountered within a protective burrow. Third, for any given species, zonation of female burrows will determine when they can search for mates. If females reside near the intertidal, they can easily dig burrows reaching damp sand or mud and expect that supplies of moisture will also be available in male burrows (even if the male is later rejected as a mate). Such females can prospect during the day and or at night if conditions dictate. On the other hand, females of extralittoral species can only search for mates at night when temperatures are low and humidity is high. For species in intermediate positions in the supralittoral, females might be able to search during the day in some locales but not in others, depending upon beach slope, depth to water level, climatic factors, and other variables. Nocturnal searching, however, should be common. Fourthly, the format of a male's display should optimise his chances of attracting a female, given the characteristics of her searching pattern. For diurnally active females, visual displays, such as waving, are optimal as a male calling signal, provided the habitat is relatively flat and unobstructed by vegetation. For nocturnally active females, acoustic calling by males is clearly best. And for supralittoral species where some females can risk daytime searches, as in *O. saratan* and *O. ceratophthalmus*, the male solution is a visual signal not requiring his extended exposure—the sand pyramid.

Viewed in this manner, the major differences between ghost and fiddler crab reproductive behaviour, and even between the less and more terrestrial ghost crabs, seem natural outcomes of a continuum of selection pressures. Whether these ideas will prove correct must depend upon the results of future studies, carried out with other species of ghost crabs residing in a wide range of habitats.

V. DIRECTION FOR FUTURE RESEARCH

This review has exposed a number of issues which remain for further study. Among the most important, in my view, are behavioural, ecological, and anatomical investigations of the fiddler crabs to clarify phyletic relationships and place patterns of display into a proper perspective. The physiology of vibration reception has only been analysed in a few species of ghost and fiddler crabs. Other members of the group, such as *Typanomerus* and *Scopimera*, possess enlarged tympana whose functional

significance is unknown. Relationships between zonation, water balance, and behaviour may provide major insights into patterns of display and their evolution. Finally, the study of female behaviour, including criteria for mate selection, orientation to sound sources, and discrimination capabilities, is ripe for further work. I hope that if nothing else the reader now understands why so many have found these animals particularly fascinating and useful as experimental subjects.

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