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 Atsaides, 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 (Gercarcinidae, 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