INTRODUCTION

Intraspecific aggressive behavior can be viewed as one of a set of response mechanisms mediating competitive interactions over some resource (food, shelter, mates) in actual or potential short supply (Wilson, 1975). The search for principles which dictate when overt aggression is selectively advantageous, or how much risk should be taken, or effort expended, in a fight now goes on (Brown & Orians, 1970; Maynard Smith, 1976; Dawkins, 1976; Hyatt, Smith & Raghavan, in press). The theoretical ideas generated have proven stimulating, but most remain to be supported by a body of observational or experimental studies.

Like most behavioral phenomena, aggression can be analyzed either in terms of its proximate or ultimate causation. One approach, which is proximate in emphasis (but has important evolutionary implications), is to examine aggression across species by techniques which permit interspecific comparisons, regardless of the behavioral modalities or context. Such comparisons should be particularly valuable in elucidating the combatant strategies, or "sets of rules," which mandate the ways in which agonistic systems vary with the value of the resource in question. Information theoretic measurements are tools which can be used to aid comparisons under these conditions.
So far, the generalizations emerging from information theory approaches have been few. In part, this is because the technique has been sporadically applied. For example, only three species of vertebrates have been investigated (Altman, 1965 — rhesus monkeys; Chatfield & Lemon, 1970 — cardinal and wood pewee). However, among the invertebrates, many crustaceans have proven especially amenable to study. These include the aggressive systems of hermit crabs (Hazlett & Bossett, 1965), mantis shrimp (Dingle, 1969), crayfish (Rubenstein & Hazlett, 1974), spider crabs (Hazlett & Estabrook, 1974), and snapping shrimp (Schein, 1975). But differences in statistical techniques, calculational errors, and the largely artificial conditions under which fighting was observed have all precluded the kinds of across-species comparisons, even within these animals, which one would like to have. In this paper we use statistical and information theory techniques to analyze the aggressive behavior of fiddler crabs. We studied two ecologically and phyletically distinct species, and witnessed their behavior in the field. Our two species show some interesting differences in their agonistic systems, which allow us to examine how evolutionary and ecological forces may be shaping information exchange between the combatants.

The animals observed during this study were *Uca pugilator* and *U. pugnax*. We selected these two species of Western Atlantic fiddler crabs because they are abundant and readily show aggression in the wild. They also have distinct habitat preferences, which we felt could be altering their aggressive behavior patterns. A description of combat acts, their frequencies, some variables which influence fight outcome, and other factors related to aggression in both species are found in Hyatt & Salmon, 1978. To our knowledge, this is the first such analysis of crustacean aggressive behavior performed with data collected in the field.

**METHODS**

I. Field methods, data sets and behavioral protocol.

Observations were made during low tide from June-August, 1975. Each pair of crabs was observed only once before they were captured, measured and removed from the population. Sequential records of each fight were recorded on audio tape, then transcribed, coded, and analyzed by computer (IBM 370/158), using source programs developed especially for this purpose. A total of 858 combat interactions were recorded (426 for *Uca pugilator*; 432 for *U. pugnax*) near the Duke University Marine Laboratory, Beaufort, NC.

Details of data collection, combat ethograms, and some basic statistical relationships were previously described (Hyatt & Salmon, 1978). For the present analysis, the protocol and data sets used in Hyatt and Salmon were changed in three ways. First, the sequential records were modified so that acts by the Resident (R), or burrow-owning crab, were alternated with acts by the Wanderer (W). This was done by adding the act “Null Move” (NM) to the sequence wherever a R-R or a W-W transition occurred. We