DOMINANCE HIERARCHIES IN THE CRAYFISH PROCAMBARUS CLARKII (GIRARD, 1852) AND THE QUESTION OF LEARNED INDIVIDUAL RECOGNITION (DECAPODA, ASTACIDEA)

BY

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INTRODUCTION

Various species of invertebrates including a cockroach (Ewing, 1974), a lobster (Fiedler, 1965), wasps (Pardi, 1948; West, 1967), hermit crabs (e.g., Hazlett, 1968), and three species of crayfish (Bovbjerg, 1953, 1956; Lowe, 1956) form linear dominance hierarchies. It is often assumed that the formation of these hierarchies depends on learned recognition of dominants by subordinates (Bovbjerg, 1956) or learned recognition of individuals (Hazlett, 1969; Lowe, 1956) as occurs in the dominance orders of some vertebrate species (e.g. Allee et al., 1959; Bernstein & Gordon, 1980; Clutton-Brock & Harvey, 1976; Wilson, 1975). Johnson (1977) has argued against this view as applied to the crayfish, and previous observations of crayfish hierarchies do not exclude other interpretations. Winston & Jacobson (1978), for example, have shown that linear dominance hierarchies in a hermit crab do not involve learned individual recognition but form on the basis of recognition of an 'aggressive state' which they define as 'the readiness with which an animal engages in agonistic interactions'. They briefly reevaluated earlier work on individual recognition in crayfish dominance hierarchies (Lowe, 1956) and found it to be consistent with their concept of recognition of aggressive state. Furthermore, they proposed that responses to aggressive state may be more generally important than individual recognition in invertebrate hierarchies.

Learning is certainly not required for the formation of linear dominance hierarchies as evidenced by the dominance order of crickets (Alexander, 1961), but alterations in the behavior of dominants or subordinates as a result of intragroup interactions may help stabilize a dominance order (Chase, 1974, 1982). Hazlett (1969) notes that 'these alterations can be either of a general nature (e.g., overall changes in aggressive drive) or can be directed toward group members, which therefore must be recognized in some way'.

Re-examination of these possibilities in a crayfish dominance hierarchy requires a more detailed analysis of the time-course of hierarchy formation than previously undertaken. Consequently, I monitored with the aid of a videotape
the formation of dominance hierarchies by the crayfish *Procambarus clarkii* to observe whether changes in intragroup interactions occur and, if so, whether they are generalized or involve changes in aggressive behavior between particular individuals or ranks as expected of learned recognition. Experiments were conducted to further examine the role of intragroup interactions in dominance hierarchy formation by *P. clarkii*. The results suggest that the formation of linear dominance hierarchies by *P. clarkii* does not involve learned individual recognition.

**MATERIALS AND METHODS**

Adult specimens of *P. clarkii* were collected locally and maintained individually until use (about one week) in plastic pans half-filled with seasoned tapwater. The crayfish were kept at room temperature (about 22°C), illuminated on a 14:10 L:D cycle, and fed several pellets of 'Gainesburger' every other day.

The four crayfish placed together in any one experiment had been collected from the same stream but from four sites separated by at least 100 m. This reduced the possibility that these crayfish had interacted significantly with each other prior to being placed in the tank for observation (Black, 1963; Hazlett et al., 1974; Merkel, 1969).

The formation of dominance hierarchies by *P. clarkii* adults was recorded on videotape. Four individually marked crayfish of similar size (carapace length, 38.7 ± 4.9 mm) were placed simultaneously into a 65 cm diameter circular tank at the outset of the videotaping session. Light was provided by one 100 W bulb positioned about two meters above the center of the tank. A loosely woven white cotton cloth covering the bottom of the tank improved traction for the crayfish and contrast for the videotape. In each experiment, the videorecorder automatically recorded 15 s of every 30 s for four hours between 2000 hr and 2400 hr on each of three consecutive nights. The crayfish were not disturbed except to supply them with food in the interim two days.

I recorded four groups of animals in this way. No individual participated in more than one experiment. All collections and experiments were conducted between June and September.

Videotape analysis included monitoring the encounters between crayfish to determine rank order, measuring the spacing between individual crayfish, and estimating the locomotory activity of individuals. An encounter was defined simply as any direct approach of one individual towards another within a distance of 30 cm. The large size of the observation tank reduced the number of incidental contacts, and virtually all encounters appeared aggressive. The individual that retreated first from an encounter was designated the 'loser'. In the very few cases when both individuals retreated simultaneously, each was scored as losing to the other. If the outcome of an encounter was not recorded