Neighbor Dislodgement and Burrow-Filling Activities by Male
*Uca musica terpsichores*: A Spacing Mechanism

N. Zucker
Department of Biology, New Mexico State University; Las Cruces, New Mexico, USA

Abstract

*Uca musica terpsichores* males sometimes dislodge their neighbors and fill in their burrow entrances with sand. Field observations and marking of individual burrows were used to determine the frequency of this activity as well as the sex and behavior patterns of the actors involved. Burrow filling is performed only by adult males which will display later on in the low-tide period. It is directed toward neighbors of both sexes. However, significantly more male neighbors were dislodged (46%) than female neighbors (28%) for distances up to 25 cm from the aggressor's burrow. For both sexes, the frequency of burrow filling increased significantly the closer they burrowed to displaying males. From these results, it is suggested that burrow filling is a primary means by which *U. musica terpsichores* males establish and maintain their territories, which they use for display purposes. A description of the burrow-filling behavior is also given.

Introduction

Members of several diverse groups of burrowing animals have been observed filling in the burrow entrances of opponents with soil during or shortly after agonistic encounters. King (1955), working with the black-tailed prairie dog (*Cynomys ludovicianus*), and Armitage and Downhower (1970), studying the yellow-bellied marmot (*Marmota flaviventris*) described instances where the dominant individuals threw dirt or rocks on top of subordinate individuals which retreated into their burrows during an encounter. Armitage and Downhower (1970) suggested that this "interment behavior" is similar to a "redirection activity", while Smith et al. (1973) interpreted this behavior as a displacement act.

Incidents of a similar behavior pattern have been reported in three species of ghost crab: *Ocypode gaudichaudii* (Crane, 1941), *O. saratan* (Linsemann, 1967), and *O. ceratophthalmus* (Lighter, 1974). In each of these three instances, however, the subordinate burrow owner was not in his burrow during the filling-in activity. Instead, he was driven away from his burrow area during an encounter with the dominant crab which then proceeded to fill in the abandoned burrow. Lighter (1974) suggested that this behavior is a spacing mechanism which permits individuals to maintain a minimum distance between themselves and their nearest neighbor.

This paper describes burrow-filling activity in fiddler crabs, another member of the family Ocypodidae. Unlike the previously reported single observations on ghost crabs, I have observed frequent occurrences of burrow-filling behavior in *Uca musica terpsichores* Crane and in several other tropical *Uca* species. This report supports Lighter's (1974) contention that burrow filling, at least in the Ocypodidae, serves to maintain minimum distances between neighbors.

Materials and Methods

Study Sites

Observations were made on two small protected intertidal sandy mud-flats along the Fort Amador Causeway just south of the Pacific entrance to the Panama Canal. No other *Uca* species were present in the vicinity of the observations.

Distribution of Adults in a Small Population

One population of the highly advanced fiddler crab *Uca musica terpsichores* Crane
consisted of fewer than 100 adults. On 21 July 1971, the distance from each adult male to his nearest adult neighbor (male or female) was measured. The males were assigned to one of three behavior categories (displaying, display/feeding, or feeding) based on the pattern of burrow and "feeding" pellets near the male's burrow (Zucker, 1973). A Kruskal-Wallis one-way analysis of variance test (Siegel, 1956) was used to test for differences between the mean values of nearest male neighbor distances in each pair of behavior categories.

Description of Burrow Filling

A much larger population on a neighboring flat 1.5 km north served as the study area in 1975. This flat was exposed during low tide for a period of only 3 to 4 h. During June, observations of the crabs' behavior were made during the early periods of low tide with the aid of binoculars. Records of interactions between individuals were obtained on 35 mm still and Super 8 mm movie film.

Frequency of Burrow-Filling Activity

Few observations of burrow-filling behavior were made during the early morning or late afternoon low tides; therefore, the following observations were restricted to low tide hours between 10.00 and 16.00 hrs. Shortly after the crabs emerged each day, markers (yellow toothpicks) were placed near pairs of burrows belonging to adults which emerged within 25 cm of each other and which had no closer adult neighbors. Next to each burrow the sex of the individual occupying it was recorded in the sand. The flat was then left undisturbed until the latter half of the low tide period, when the following were recorded: (1) the distance, to the nearest cm, between each pair of marked burrows; (2) the sexes of the individuals involved; (3) the burrows which remained opened and those which were filled in; (4) the predominant behavior of the crabs whose burrows were still open (based on burrow patterns; see Fig. 1). The date, hour of low tide, air and substrate temperatures and weather conditions were also noted. In order to analyze the data, one major assumption had to be made. When a burrow was filled in it was assumed that the nearest adult male was responsible for it. This assumption is based on numerous observations of burrow filling in which males approached their nearest neighbor and engaged it in an encounter. Females and young were never observed to fill in burrows. The data were pooled for each 5 cm interval from 0 to 25 cm.

A chi-square test was used to determine whether there were differences in frequency of burrow filling at the different nearest neighbor distances. A chi-square check was also run to determine whether burrows of one sex were filled in more frequently than those of the other for each of the distance intervals.

Results

Distribution of Adults in a Small Population

Table 1 shows that neighbors of male Uca musica terpsichores displaying (waving their major cheliped) exclusively were not significantly further away than neighbors of males which both displayed and fed (P >0.80). However, neighbors of both displaying and display/feeding males were significantly further than neighbors of feeding males (P <0.01 and <0.05, respectively). These results suggest that some type of spacing mechanism is at work.

The remaining observations were undertaken in order to verify this suggestion and ascertain the nature of the spacing mechanism. Since no difference was found between neighbor distances of displaying and display/feeding males, these behavior categories have been pooled in all further observations. These males will, henceforth, be referred to as displaying males.

Description of Burrow Filling

The crabs began emerging each day within 15 to 30 min after the diurnal tide receded. Upon first emerging the crabs usually fed. Those males which would display later in the low-tide period fed at least 10 cm from their burrow entrances. As a result, a circular area of 10 cm radius around their burrows was kept clear of all "feeding" pellets (2 mm pellets of filtered discarded sand, see Fig. 1). This clear area served later in the low-tide period as the male's territory (defended display ground). Non-displaying crabs (all females, juveniles and some males) discarded "feeding" pellets immediately in the vicinity of their burrow entrances (Fig. 1). As more crabs emerged, increased agonistic activity occurred. Males often challenged both neighboring males and females. Encounters between two males