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Abstract

A BEHAVIORAL AND ECOLOGICAL STUDY OF THE FIDDLER CRAB UCA CRENULATA

by

Magali Hantson-Parker

The social interaction and behavioral activities of a population of fiddler crabs, Uca crenulata, located in the "Aqua Hedionda" lagoon in Carlsbad, California, is the subject of this study.

Variations in environmental factors as well as seasonal behavioral changes cause an important fluctuation in the male to female ratio and in population density.

A daily and seasonal variation is observed in the different behavioral activities displayed by the crab colony and are caused by biotic and abiotic environmental factors and by intrinsic hormonal changes.

A male color variation from dark to light is related to behavioral changes during the breeding season. This lightening of the carapace, most likely caused by sexual hormones, is a thermoregulatory advantage for the mating male.

Studies of the waving behavior of the light colored male in presence of a female, shows wave periods ranging from 1 to 5 seconds. The rate of the wave's major component

corresponds to the optimum stimulus speeds (30-50 degrees/sec.) of a rate sensitive neuron found in the optic nerve of the crabs. These results show a strong relation between behavioral data obtained on the field and physiological data concerning movement and rate selective neurons in the eye of the crab *U. crenulata*.

The identification of 9 different stages in the egg development of *U. crenulata* as well as the time necessary to complete the incubation shows that the breeding cycle length is 2 weeks.

LOMA LINDA UNIVERSITY

Graduate School

A BEHAVIORAL AND ECOLOGICAL STUDY OF THE FIDDLER CRAB *UCA CRENULATA*

by

Magali Hantson-Parker

A Dissertation in Partial Fulfillment of the
Requirements for the Degree
Doctor of Philosophy in Physiology

June 1985

Each person whose signature appears below certifies that this dissertation in his opinion is adequate, in scope and quality, as a dissertation for the degree Doctor of Philosophy.

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INTRODUCTION

Intertidal Zone

The intertidal zone is a region of environmental instability, with large changes in temperature and salinity. The time-period of changes varies with day-night cycles, lunar cycles and seasonal cycles (Vernberg, 1969).

Sandy beaches located in lagoons or estuaries have different environmental characteristics than sandy beaches facing the open ocean and the strong wave actions. Muddy beaches, sandy beaches or rocky shores each produce different environmental stresses on the crab, due to variation in substrate, food resource, drainage and predation.

Crab Distribution and Life History

The adult fiddler crab can be found in different types of habitats, from muddy to sandy substrates.

The genus _Uca_ is widely distributed in temperate and tropical regions, on the intertidal zone of the coast. The life history of _Uca_ includes the following stages (Vernberg, 1969): (1) The adult lives in a semi-terrestrial habitat and the ovigerous female carries fertilized eggs on the ventral surface of the abdomen; (2) free-swimming zoeae hatch from these developing eggs, and one observes normally five distinctive zoeal stages; (3) the fifth zoeal stage metamorphoses into a megalopa which molt into the young crab stage.

Rhythmic Behavior

Fiddler crabs inhabiting the intertidal zone must adapt their activities to day-night cycles and tidal cycles. The tidal cycle imposes on the animals a rhythmic alternation between terrestrial and marine periods of existence. At the same time the crabs are influenced by the day-night cycle, since they exhibit specific diurnal and nocturnal habits (Barnwell, 1968).

The general pattern of activity of intertidal fiddler crabs is well known. As their habitat is exposed by the ebbing tide, the fiddler crabs emerge from their burrows onto the surface, and can be observed feeding, repairing burrows, fighting or courting. The crabs withdraw into their burrows with the return of the tide. The animals may appear to anticipate the tide by entering and plugging their burrows before the water reaches them (Altevogt, 1957) or they may stay on the surface and continue to display under several inches of water (Teal, 1959).

Sexual Discrimination in Uca

Interspecific Discrimination

In 1971, Aspey investigated the factors responsible for interspecies sex recognition and conflict in *U. pugnax* and *U. pugilator*. Dead individuals were used to stimulate courtship behavior as well as antagonistic behavior in populations of both species. Both species failed to distinguish between conspecific females and males lacking their major cheliped. This shows that sexual recognition depends in part on the presence of the major cheliped. U. pugnax males distinguished between conspecific and conterspecific females while U. pugilator did not discriminate between females of different species, and responded to both with typical courtship behavior. These differences in behavior could be explained by a difference in male-female interaction in the two species. In the case of U. pugnax, the male could make the choice in selecting mates, while female would make the choice in U. pugilator.

Intraspecific Discrimination in U. pugilator

The presence of a major cheliped is the critical factor in sexual discrimination (Salmon, 1965) but some courtship of conspecific males lacking a major cheliped was observed by Burkenroad (1947).

Sexual discrimination is mediated by visual cues at close range during the day and is probably mediated by tactile cues and sound production at night or in the burrow (Salmon and Atsaides, 1968).

Male U. pugilator exhibits courtship waving to any female stimulus. The waving behavior consists in a movement of elevation and lowering of the major chelae (Crane, 1957).

Female _U_. _pugilator_ detects rapping sounds produced in courtship by conspecific males (Salmon, 1967; Salmon and Atsaides, 1968). Courting males produce rapping sounds by beating the ventral or outer surface of their flexed major cheliped against the substrate immediately adjacent to or just inside the burrow entrance (Salmon, 1965). The female _U_. _pugilator_ responds to substrate vibrations that are produced when the male rapps (Salmon and Horch, 1972).

Color Changes

Introduction

The use of color in nature has interested scientists for many years, but it was not until 1940 that Cott established clearly that the color patterns of animals are used in communication. It is now general knowledge that natural colorations of animals are used in mimicry, in concealment, for sexual attraction or agonistic display. Tinbergen, in 1953, showed that color patterns frequently act as visual "releaser" sending key stimuli which evoke an appropriate response in the reacting animal.

Mating display. During the breeding season, males display specific colors to increase their conspicuousness to the females. In diurnal animals, display colors are bright while in nocturnal animals they are light. The significance of color pattern to successful mating is less common in mammals than in birds and some other taxa. The display of nuptial coloration suggests that during the breeding season, the need for a concealing coloration has less importance than the display color necessary to attract females. Because of his role in sexual selection, the male, tends to be more colorful than the female who needs protection during gestation and while taking care of the young. For these reasons, there is a marked sexual dimorphism between male and female color patterns. Darwin (1871) was the first to notice the meaning of this color dimorphism which is observable in the different members of the animal kingdom.

Mechanisms Involved in Color Change

Chromatophores. Cells that disperse or concentrate pigment, and thereby change the tint of the organism, are known as chromatophores. They may be close to the surface or deep, surrounding various organs (Fingerman, 1963). The term "color change" is not accurate because, in most cases, the color of the animal does not change but merely its shade or tint. Chromatophores are classified according to the pigment or pigments contained therein. If the pigment is brown or black, the cells are referred to as melanophores. Yellow chromatophores are called xanthophores and red ones, erythrophores.

The shade of an organism depends on:

--the number of chromatophores,

--the nature of pigments contained in each chromatophore,

--the degree of dispersion of contained pigments.

Color changes have been divided into two categories: morphological and physiological. The former implies a change in the quantity of pigment, while the second involves alteration in the degree of granule dispersion in the chromatophore. Morphological color changes are usually stimulated by a specific background while physiological changes may be evoked by light and temperature.

Color changes in crustaceans. Color change in response to light, darkness, and background tint is found in vertebrates (fish), insects and crustaceans (Pouchet, 1872; Perez, 1929).

The response of a chromatophore to light is divided into two categories: (1) Primary effect--light acting directly on the chromatophores causes expansion of pigment, while in its absence, the pigment contracts (Keeble and Gamble, 1904); (2) Secondary effect--light reflected from the light colored surroundings acts on the eyes with the result that a hormone is liberated into the blood from glands in the eyestalks. This hormone causes pigment contraction in the chromatophores (Perkins, 1928). A black background, through optical stimulation, causes another hormone to be liberated from the rostral gland, resulting in pigment expansion. In crustaceans the chromatophores receive no direct innervation. Their secondary response is therefore determined only by hormones. These hormones are known to be secreted by the sinus gland of the eyestalk and by elements within the central nervous system.

Color changes in Uca--General Concepts. In brachyuran crabs, most external pigment is located in monochromatic chromatophores which are found chiefly in the epidermis (Crane, 1944). Four pigments occur in crab chromatophores and they are all found in Uca: Black or brownish-black, red, yellow and white. All of the striking specific color differences observed in fiddler crabs may be explained by the assumption that each species contains these pigments in varying proportions, distribution and state of dispersal (Crane, 1944).

The two sources of hormones in fiddler crabs are the sinus gland of the eyestalk and the central nervous system organ.

Factors influencing color changes. Experiments on Uca pugilator furnish us with a detailed description of factors influencing the color changes (Crane, 1944).

Uca pugilator, studied by Abramowitz (1937), shows a 24-hour rhythm of color change which is characterised by a pale phase at night and a dark phase during the day. The pale phase is a result of concentration of black and white pigments, while the dark phase is the result of dispersion of both pigments. This rhythmic color change is abolished by removal of both eyestalks (Carlson, 1935, 1936). On a white background, <u>Uca pugilator</u> possesses a specific background response which concentrates black pigment and disperses white pigment, while on a black background, black pigment is dispersed and white pigment is concentrated (Brown and Sandeen, 1948). The dispersion of white pigments increases as the intensity of the illumination increases. This may be a reaction to protect the animal's protoplasm (Brown and Sandeen, 1948). These responses which are superimposed on the daily rhythm would appear to have a thermoregulatory function because, during intense sunlight, concentration of black pigment would diminish the area which maximally absorbs radiant energy, whereas dispersion of the white pigment increases the area which reflects radiation (Wilkens and Fingerman, 1965). Temperature measurements on dark and pale crabs show that pale crabs maintain themselves about 2°C cooler than dark crabs. Blanching seems to be a useful survival mechanism since temperature of 42°C results in death (Wilkens and Fingerman, 1965).

Color changes in <u>Uca</u> populations are induced by changes in illumination, temperature and background.

Crane (1941, 1944) suggests that the breeding season has the most pronounced effect on crab color variations.

After emergence in the morning, the courting male of *U. stylifera* changes from dull gray to pure white with a brief intermediate phase in which the carapace is brilliant yellow. Another striking example of color change is found in *U. latimanus*: The carapace of the displaying males becomes pure white each day, but only after feeding and burrow building activities are completed. In both species described below, the display coloration is lost when the crabs are captured (Crane, 1941). In summary, whiteness of the breeding fiddler crab is assumed seasonally for most species and daily for certain individuals (Crane, 1941). But lightening of the carapace during the breeding season is not an absolute rule for the genus *Uca*. In *U. pugnax*, dark displaying males are the rule and the lighter phase is the exception (Crane, 1944).

This lightening of the crab carapace during the breeding season is possible only if there exists a putative chromatophoric action that compensates for, or masks the normal rhythmic color changes. The three chromatophoric actions suggested by Crane (1941) are:

--inhibition of normal diurnal expansion of the black pigment,

--dispersion of yellow pigment,

--dispersion of white pigment.

It is not known if a separate hormone is responsible for each mechanism.

Rationale and Objectives

Electrophysiological studies on the eye of *Uca crenulata* has shown that specific visual neurons are stimulated or respond optimally to discrete aspects of the mating behavior sequence. The purpose of this research is to examine and describe the ecology and behavior of *Uca crenulata* in an attempt to relate the sensory neuron activity (Rafuse, Hall in preparation) to the *Uca crenulata* behavior.

The absence of ecological and behavioral studies on the crab *U. crenulata* made a study of this nature of primary importance. The presence of an active and growing population of crabs at Carlsbad, California, provided the ideal location for this study which includes: (1) Ecological and environmental factors affecting the spatial and temporal distribution of the crab *U. crenulata*. The environmental factors considered are substrate texture, temperature, topography and community interactions. The purpose for these observations was to consider possible reasons for the rapid growth of a *Uca* population in this area. (2) The relation of tidal rhythm, day-night cycle and season to crab behavior. The activities observed in this study are feeding, burrow building, fighting and waving. (3) The color changes during the breeding season are a complex phenomena and involve only part of the population. Observations were made in the field to determine the usefulness and the mechanism responsible for this change. (4) The mating behavior, well described in several species of fiddler crabs by Crane (1941, 1975), is compared with the Uca crenulata mating behavior. Waving behavior in particular is studied in an attempt to understand its importance in mate selection. (5) The pattern of the breeding cycle is determined in two ways, first by timing the cycling of gravid females in the field and second by correlating this with a study of their eggs development.

The principal reasons for the selection of this project are, the absence in the literature of an ecological or behavioral study of Uca crenulata and the possibility of a physiologically explained behavioral activity.

MATERIALS AND METHODS

Study Site

This research was conducted from June 1981 through December 1982. The study site was a lagoon located in Carlsbad, California and named "Aqua Hedionda." The original lagoon has been divided into 3 smaller lagoons by man's constructions the Coast Highway, the Santa Fe railroad and Interstate 5. Part of the shore located on the north side of the second lagoon was selected for this study. The area chosen for the study site consists of 288 square meters and includes the area from the north bank to a tide level of 2.0 feet. Specific areas were chosen and marked into square meters to allow consistent counts of population density and the observation of changes in population repartition over the area during the two years of observations. A surveyor's transit was used to measure the elevation of the study site and the tide levels for each specific site in the study area (Figs. 1 and 2). The temperature of the study site was recorded for the air, surface and ground (15 cm below surface) (Figs. 3 and 4) during each period of observation.

Observation of Crabs

Field Observations

The observation site was located one meter above the colony site. This permitted observations to be made without

Figure 1. Contour map of study site in 1981.

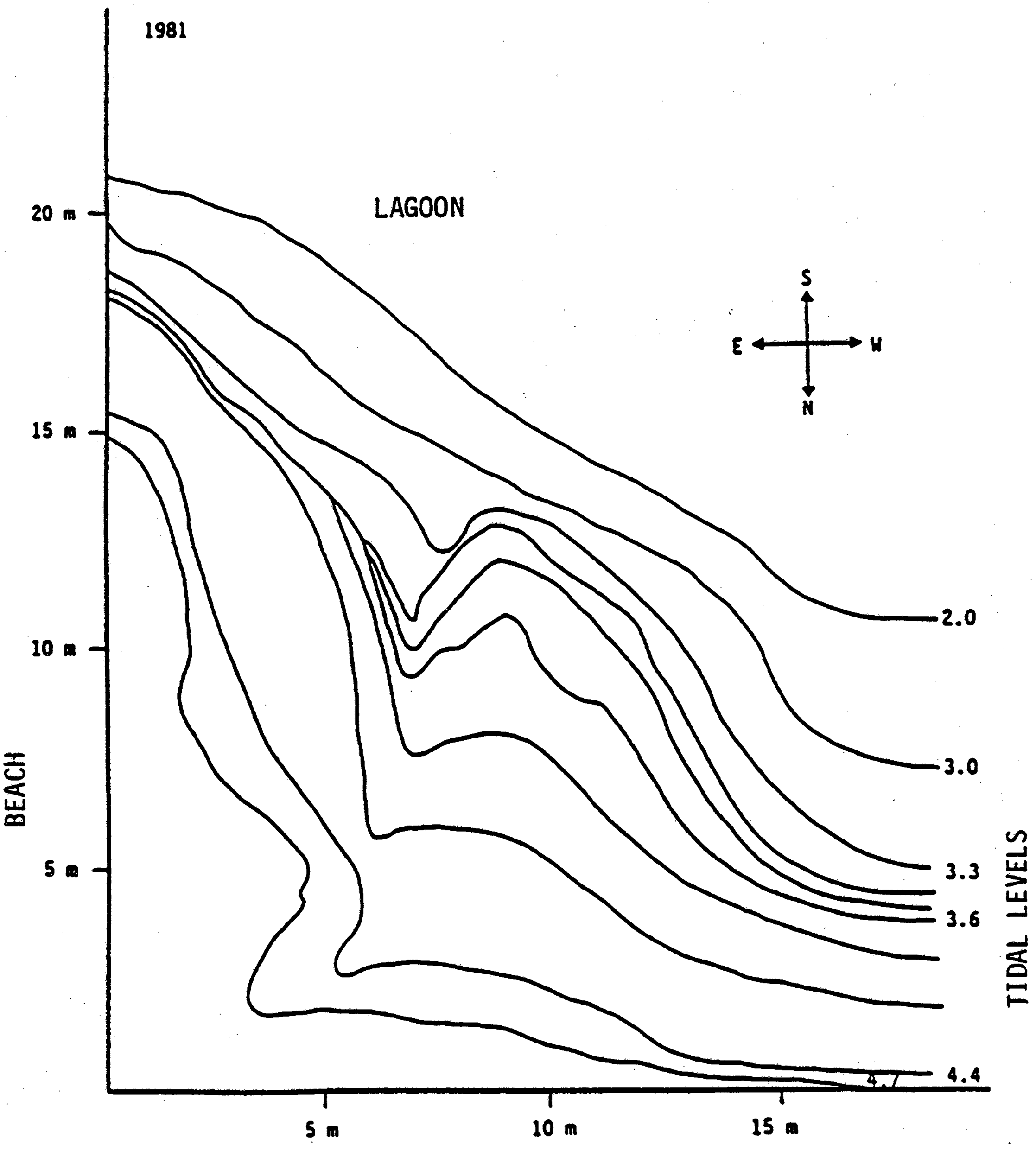

1981
LAGOON
S
E
W
N
20 m
15 m
10 m
5 m
BEACH
2.0
3.0
3.3
3.6
4.4
4.7
TIDAL LEVELS
5 m
10 m
15 m

Figure 2. Contour map of study site in 1982.

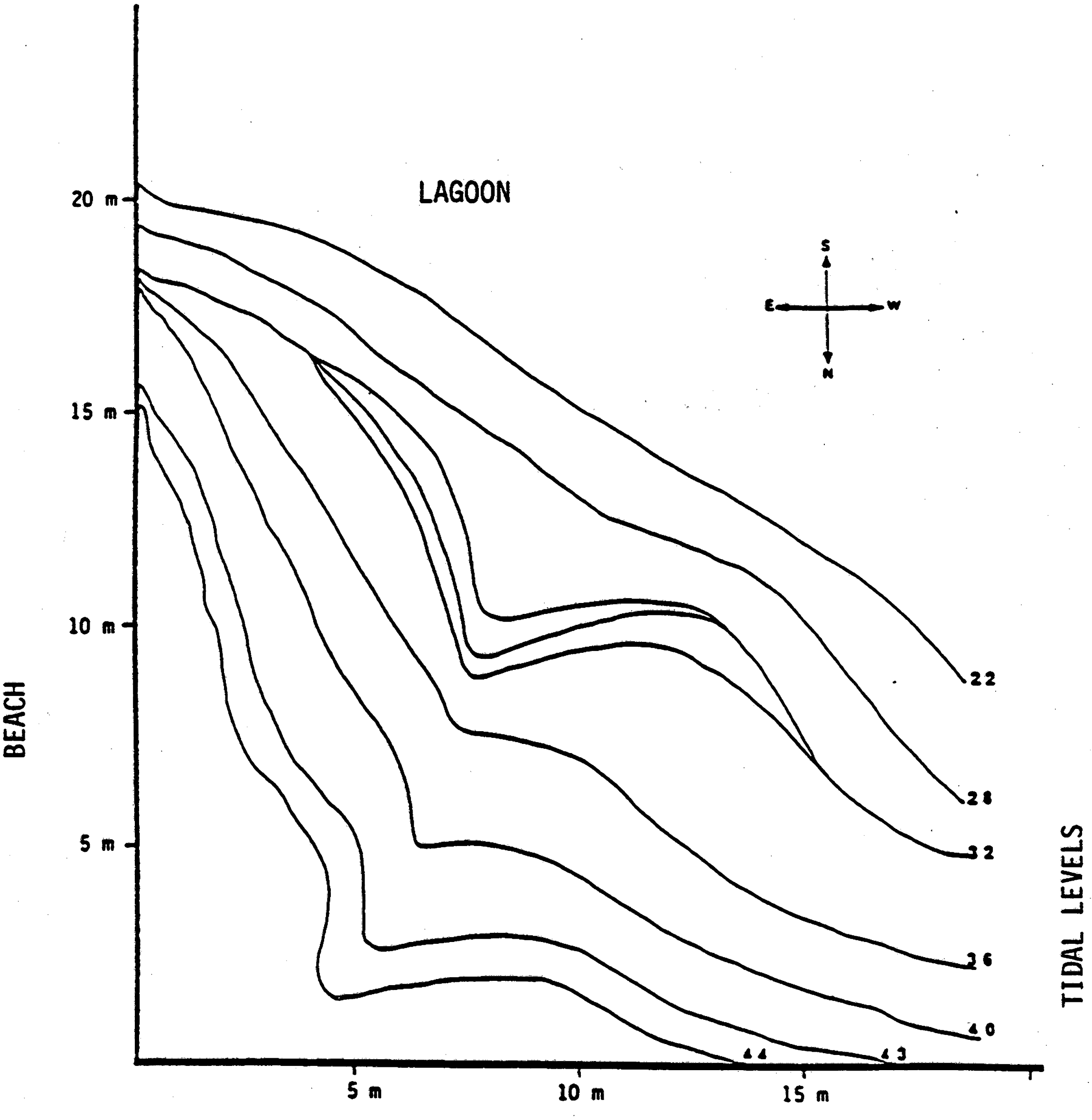

LAGOON
S
E
W
N
20 m
15 m
10 m
5 m
BEACH
TIDAL LEVELS
22
28
32
36
40
44
43
5 m
10 m
15 m

Figure 3. Daily temperature changes for July 1982 (in the lagoon). Mx. t° = daily maximum air temperature; Mn. t° = daily minimum air temperature (in Carlsbad).

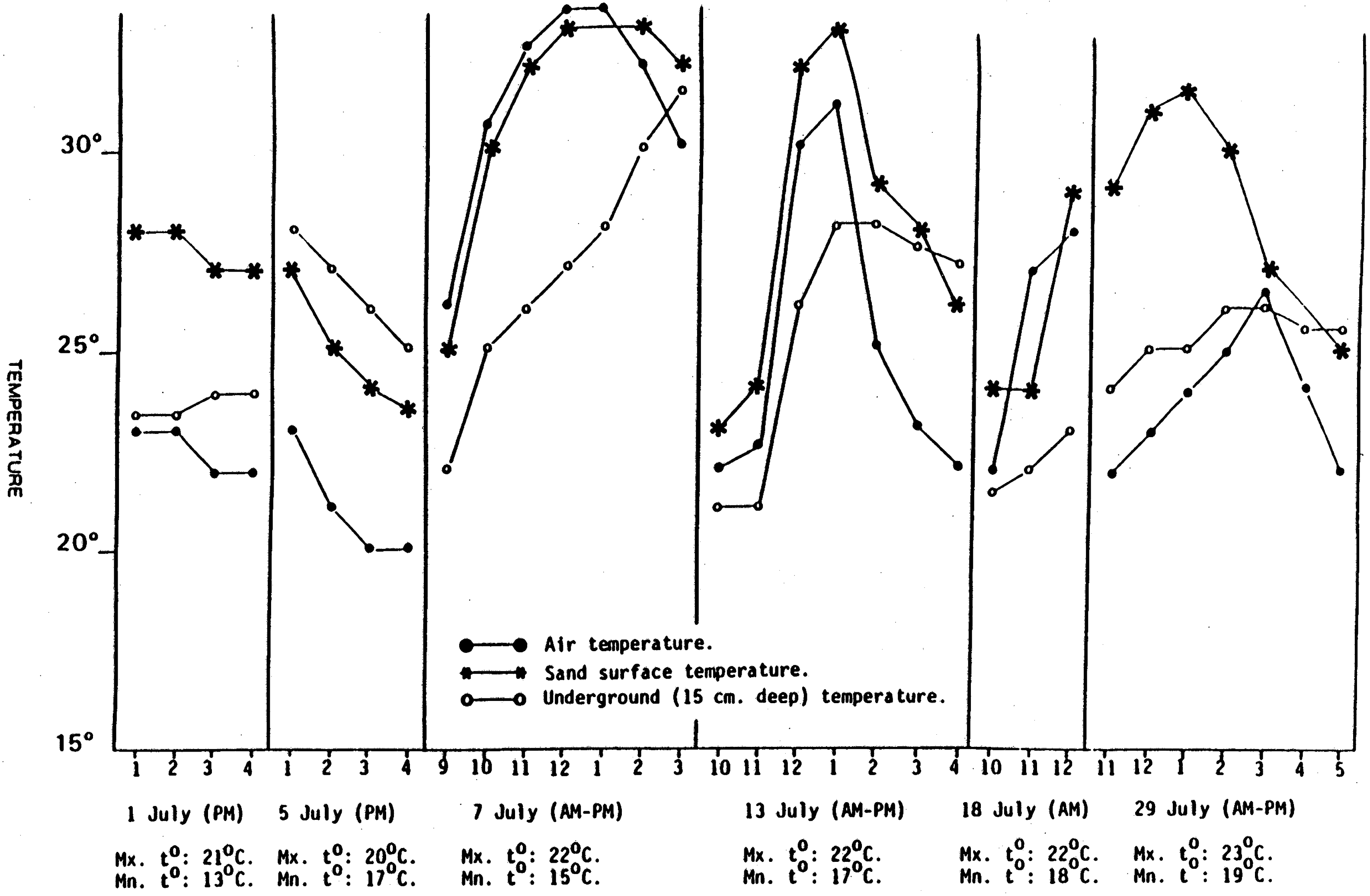
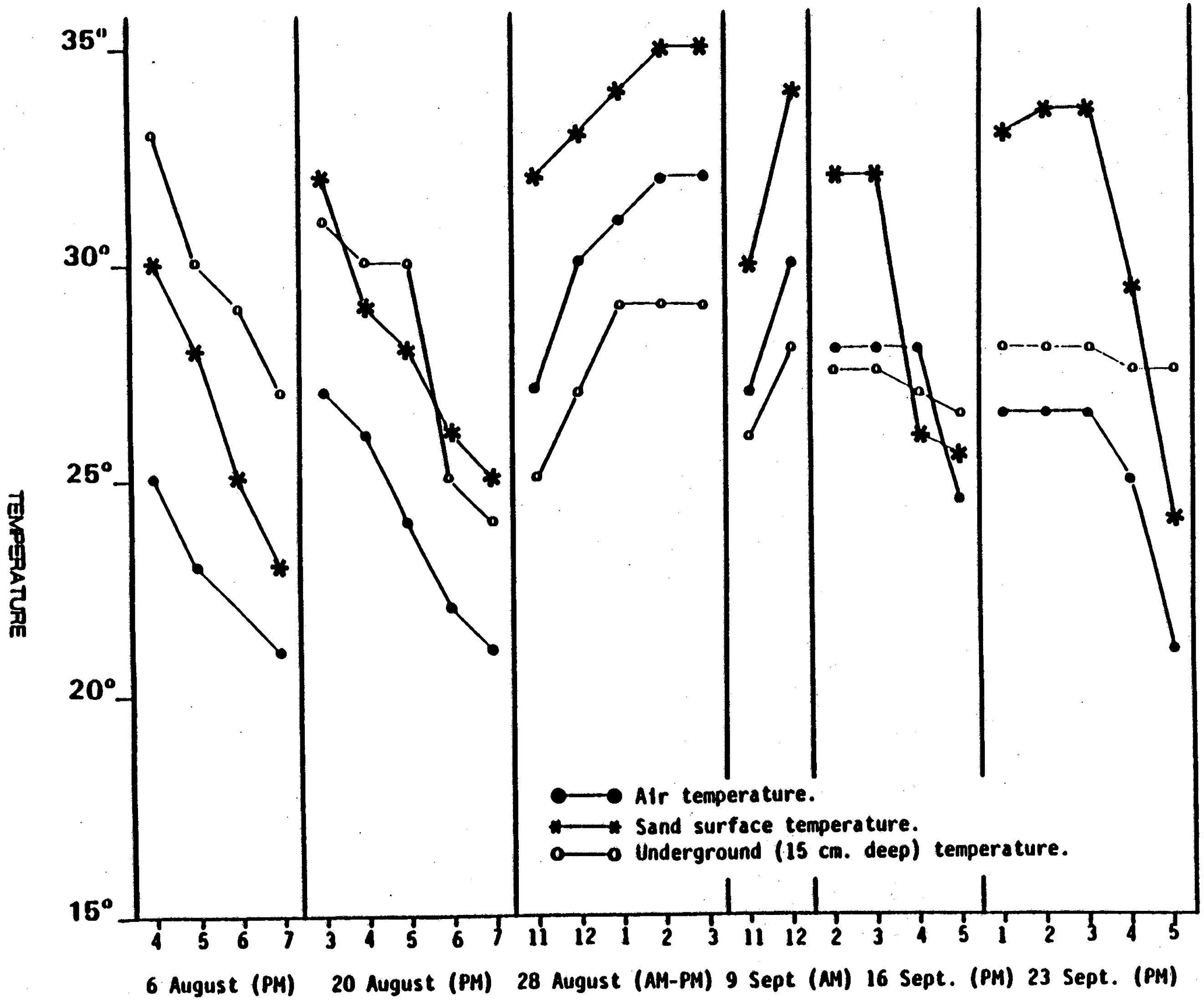

TEMPERATURE
30°
25°
20°
15°
Air temperature.
Sand surface temperature.
Underground (15 cm. deep) temperature.
1 2 3 4
1 2 3 4
9 10 11 12 1 2 3
10 11 12 1 2 3 4
10 11 12
11 12 1 2 3 4 5
1 July (PM)
5 July (PM)
7 July (AM-PM)
13 July (AM-PM)
18 July (AM)
29 July (AM-PM)
Mx. t°: 21°C.
Mn. t°: 13°C.
Mx. t°: 20°C.
Mn. t°: 17°C.
Mx. t°: 22°C.
Mn. t°: 15°C.
Mx. t°: 22°C.
Mn. t°: 17°C.
Mx. t°: 22°C.
Mn. t°: 18°C.
Mx. t°: 23°C.
Mn. t°: 19°C.

Figure 4. Daily temperature changes for August and September 1982 (in the lagoon). Mx. t° = daily maximum air temperature; Mn. t° = daily minimum air temperature (in Carlsbad).



Mx. t°: 25°C. Mx. t°: 24°C. Mx. t°: 23°C. Mx. t°: 24°C. Mx. t°: 23°C. Mx. t°: 24°C.
Mn. t°: 18°C. Mn. t°: 12°C. Mn. t°: 18°C. Mn. t°: 20°C. Mn. t°: 19°C. Mn. t°: 15°C.

disturbing the crabs. Most observations were made during the day and binoculars were used when necessary for more precise observations. A 35mm camera and an 8mm (Nikko) movie camera were used to document behavior activities related to mating and display behavior.

Laboratory Observations

A population of both males and females of *Uca crenulata* was brought to the lab and raised in a control chamber that allowed continuous observations. The chamber was equipped with lighting that permitted the simulation of dark/light cycles, precise temperature controls and the ability to simulate tide patterns. The crabs were fed with the commercially prepared fish food, Tetramin, during periods of ebb tide simulation.

Methods for Marking and Measuring Crabs

Carapace width is commonly used to classify crab size. Males and females were divided into 3 categories characterized by <0.5 cm for the small crabs, 0.5-1 cm for the medium, and >1 cm for the adults. A variety of methods were used to mark the crabs: paint, enamel, glue and tags. The combination of glue and tags provides the best long-term marking system. However, even with this system, identification is lost during the molt.

Burrow Observations

Coded sticks were placed at the burrow's entrance, marking the burrow site and depth. Burrow shape was determined by making plaster of Paris casts of the burrow.

Data Analysis

Extensive field notes were taken and the data condensed and charted with the use of an HP calculator. Behavioral data were recorded on 35mm slides and 8mm movies. The 8mm film was then projected on a screen for analysis and documentation. The waving behavior was studied in detail with a frame freeze (ELMO sound ST-1200) projector permitting a frame-by-frame analysis and reproduction of each movement studied. The speed of the movie picture used was 24 frames/ minute allowing precise observation and timing of all behavioral sequences studied.

Soil samples taken in the field were analyzed with the Bouycous method, a technique used for the mechanical analysis of soils. Samples of 100 gr of soil were mixed with distilled water and the material in suspension was measured at various times with the use of a hygrometer. This method yielded the percentage of sand, silt and clay in each sample (Bouycous, 1928).

The Carlsbad tide tables were used to match field observations with tidal pattern of the lagoon.

A microscope (Wild Heerbrugg) was used to verify the systematic data given by Crane (1975). A drawing scope (Zeiss) was used to observe and draw the stages of the eggs.

A formula commonly used in ecology to determine community quality, the Community Quality Index (CQI) as proposed by Johnson and Vasek, et al. (1975) was adapted to the crab population of Carlsbad and gives the population index (PI) for light (L) and dark (D) males forming the colony, as follows:

$$\text{PI (D)} = \sqrt{\text{\% of dark males x \% of total male population}}$$

$$\text{PI (L)} = \sqrt{\text{\% of light males x \% of total male population}}$$

PI values range from zero to ∞, i.e. for PI (D), the greater the number, the more dark males there are in the community compared to the light males.

ECOLOGICAL STUDY OF UCA CRENULATA

Introduction

The separation of the original lagoon into smaller lagoons provides the tide conditions necessary for U. crenulata development. The breakwater provided by the freeway and railroad construction breaks the tide force and protects the mud/sand shore from rapid and extreme changes. The tide covering the observation site occurs 1 hour to 1½ hours later than that predicted from the local tide tables. The tidal pattern in the lagoon produces a high high, low high, high low and low low tide approximately every 24.7 hours. The tide is one of the most important factors in regulating the activities of Uca crenulata. Their behavior follows a pattern that is dependent upon each tide cycle.

Uca crenulata is the only Uca found in the eastern Pacific, north of the Mexican border. It has become scarce in California (Crane, 1975). However the ideal situation has been created by the man-made lagoon at Carlsbad, as it provides the necessary tide and soil requirements for Uca survival. The shores are inhabited by a large and growing population of Uca crenulata. Crane (1975) mentions that most of the fiddler crabs live in intertidal zones or sheltered bays and estuaries with sandy mud or muddy substrate. In 1977 the population of Uca crenulata of the

Aqua Hedionda lagoon was found only in a few square meters, near the site of this research (Rafuse and Hall, personal observation). The topography and the soil texture of this area appear to be ideal for the establishment of a Uca crenulata colony. By 1981 the Uca crenulata population had spread to all the sand/mud beaches of the second and third lagoons.

Communities

The interaction between the biological components of an area forms a unit which is referred to as a "community".

Associated Vegetation

The mud-sand beach is bare up to the supralittoral zone which is covered with seacorn (Salicornia anthophyta). As the tide goes out, brown algae may cover the sand and these two different types of vegetation provide habitat, food and protective cover for Uca crenulata. When the layer of brown algae becomes thick it tends to suppress behavioral activities by keeping the burrow entrance dark and wet, causing the crab to remain inside the burrow. Some large eucalyptus trees on the north bank of the study site produce shade on one-third of the study site during the afternoon and this variation in exposure and temperature has a marked influence on the behavior of the crabs in the area.

The northern border of the study site has a sandy bank which rises 50 cm above the shore, then slopes 30 degrees up to the surrounding trees. Thick grass covers this area. The bank profile, the vegetation, and tide level influence the deposits left on the sand during the ebbing tide.

Animal Associates

Animal associates of *Uca crenulata* are divided into two categories:

Predators. Other than man, the crab *Pachygrapsus* and a few shore birds are the only predators. *Uca crenulata* is most vulnerable when feeding away from its burrow, in the intertidal zone. The long-beaked shore birds prey on surface feeding animals only occasionally by digging crabs out of their burrows, while *Pachygrapsus* preys on the crabs walking on the surface during ebb tide. The birds have a preference for females (75% females versus 25% males). This differential predation on the sexes by the white ibis, has been noted by Christy (1980) for *Uca pugilator*. *Pachygrapsus*, on the other hand, does not show any preferences. They eat both females and males. *U. crenulata's* major chela can be dangerous to the predator especially when inserted into the abdomen, in some cases, causing the death of *Pachygrapsus*.

Fishermen use *Uca crenulata* as bait but the location of the study site with a steep cliff on the north and west border and a fence on the east side protects the colony from most human predation. Predation of *Uca crenulata* is negligible when you consider the rapid growth of this colony.

Food. Uca crenulata eats microscopic organisms found on the sand grains and may also prey on insects such as butterflies and flies. Some invertebrates such as molluscs and worms are sympatric to Uca crenulata. These live on the surface or under the sand and contribute to the biological richness of the substrate.

Topography

Topographic measurements of the study site were taken twice during the two years of field observations. Figures 1 and 2 show the results of the two topographic transects. Elevation variation of the area during the year of observation and the changing profile of the study site are responsible for the repartition of the crab population during this period. The erosion on the lagoon, due to tidal action, is not as strong as on the open shore but did cause an elevation change at the highest point of the study site from 4.7 feet to 4.4 feet, as well as a 60 cm retreat of the bank during the twelve months of observations. The elevation profile changes due to erosion caused a smaller angle of slope on the site. Soil composition changes brought about by bank erosion (See the soil texture tables for colonies I, II and III in 1981 and 1982), and new deposits on the shore retarded the drainage of the study site.

These changes resulted in portions of the colony remaining wet, suppressing breeding and decreasing behavioral activities.

Temperature

Semi-terrestrial poikilotherms require adequate mechanisms to survive extremes of temperature greater than those found in an aquatic environment (Wilkens and Fingerman, 1965).

"The paucity of semi-terrestrial Brachyura in the temperate zone may be due to the failure of many species to evolve adaptations to perform requisite life processes at temperature below 20°C, or the lack of resistance-adaptations necessary to survive the low temperature of winter" (Vernberg, 1968).

Fiddler crabs are generally active and feeding during the ebbing tide. During the warm months of the year, fiddler crabs can be exposed to high temperatures which are near their lethal level (Teal, 1958). Behavioral adaptations to these extreme temperatures can be observed in the various *Uca* species: Crabs such as *Uca pugilator* adapt to the fluctuating environment by physiological color changing, wetting the body surface or orienting toward the sun (Smith and Miller, 1973). The blanching of fiddler crabs at high temperatures has a thermoregulatory role. Pale crabs can maintain themselves 2°C cooler than dark crabs. Wilkens and

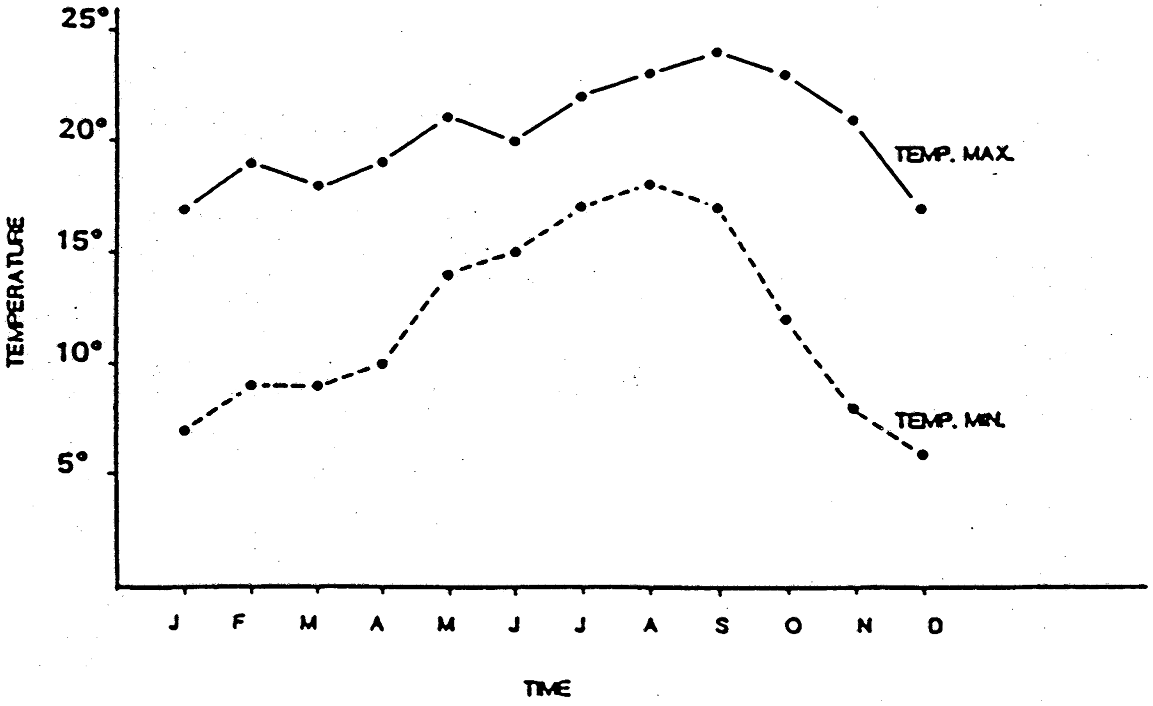
Fingerman (1965) show that at each of several wavelengths of visible light (4000 to 7000 Å), the quantity of light reflected from the dorsal surface is greater in pale crabs than in dark ones.

Uca rapax does not thermoregulate by changing color but changes temperature by retreating into the burrow or moving to the shade (Smith and Miller, 1973).

The upper and lower lethal body temperature can be approached by both U. rapax and U. pugilator during the year and the behavioral adaptations mentioned above are necessary for the survival of the species. Passano (1960) shows that low temperature blocks molting in Uca pugnax. Proecdysis duration is shortest at 29 to 32°C while at 15°C or below, proecdysis initiation is completely blocked. The temperature which blocks proecdysis initiation also blocks basal limb bud regeneration, showing again the important effect of temperature on the fiddler crab life and survival.

Fiddler crabs are strongly influenced by temperature, both in their distribution and in their seasonal activities. Reproduction activity is confined to the warmest months, and most of the crabs hibernate during cold weather (Crane, 1975). Seasonal and daily temperature changes of the air and the sand influence the behavior and population density of Uca crenulata. Figure 5 shows the maximum and minimum temperature averages for each month of the year 1982. The

Figure 5. Maximum and minimum temperature average for each month of the year 1982. The temperature is represented in Celsius. The temperature data were obtained at the National Meteorological Station at Oceanside.


25°
20°
15°
10°
5°
TEMPERATURE
TEMP. MAX.
TEMP. MIN.
J
F
M
A
M
J
J
A
S
O
N
D
TIME

crabs have the ability to adapt to high temperatures by the blanching process or frequently retreating into the burrow. However, low temperatures have a much greater influence on behavior, as they slow down or stop proecdysis and reproduction. Because of this, the minimum temperature curve is of primary importance in our discussion. The increase in temperature from May to August coincides with physiological and behavioral changes characteristic of the breeding season.

Temperatures were recorded from the air, the ground surface, and an area 15 cm below the surface (Figs. 3 and 4). The air and ground surface temperatures vary considerably during a daytime recording, as these temperatures are influenced by fog, cloud cover and wind currents. The underground temperatures are more constant (never reached the surface temperature of 35°C) and represent the ambient temperature of the burrows. It is evident that the temperature fluctuations, both seasonal and daily, are reflected by the behavioral activity of this crab.

Substrate Analysis

Soil consistency as well as population distribution on the study site is not homogenous. A better understanding of the soil texture is helpful in explaining the crabs' preference for certain areas. The method used showed that the soil texture at the surface is constant (86 ± 2% sand in 1981, and 85 ± 2% in 1982). When soil samples are taken at a depth of 15 cm, which corresponds to the mean depth of the burrow breeding chambers, there is a noticeable difference. The results obtained for the year 1981 and 1982 are shown in Figures 6 and 7 and indicate that the permanent mating colony prefers sandier areas in which to build their burrows. Soil containing 84 ± 2% sand at a depth of 15 cm is necessary for breeding burrow construction. In areas located between the mating colonies, the percentage of clay and silt is 8% higher; therefore, the soil is muddier and contains less oxygen. This may explain the absence of breeding burrows. Temporary burrows used during high tide by a portion of the crab population are the only burrows located in the muddier soil. The soil consistency appears to be important for *Uca crenulata's* presence in the lagoon and for the building of breeding burrows.

Figure 6. Soil texture analysis for the permanent and temporary burrow location in 1981. Permanent and breeding burrows are located in colonies I and II while the temporary burrows are found between these areas.

SOIL TEXTURE ANALYSIS, 1981
(samples 100 gm)

Sample Location		% Sand	% Clay	% Silt
Colony I	Top 1 cm	88.2	9.4	2.4
	15 cm deep	86.7	9.6	3.7
Between	Top 1 cm	86.2	11.3	2.5
	15 cm deep	79.2	10.3	10.5
Colony II	Top 1 cm	85.4	11.6	3.0
	15 cm deep	86.4	11.1	2.5

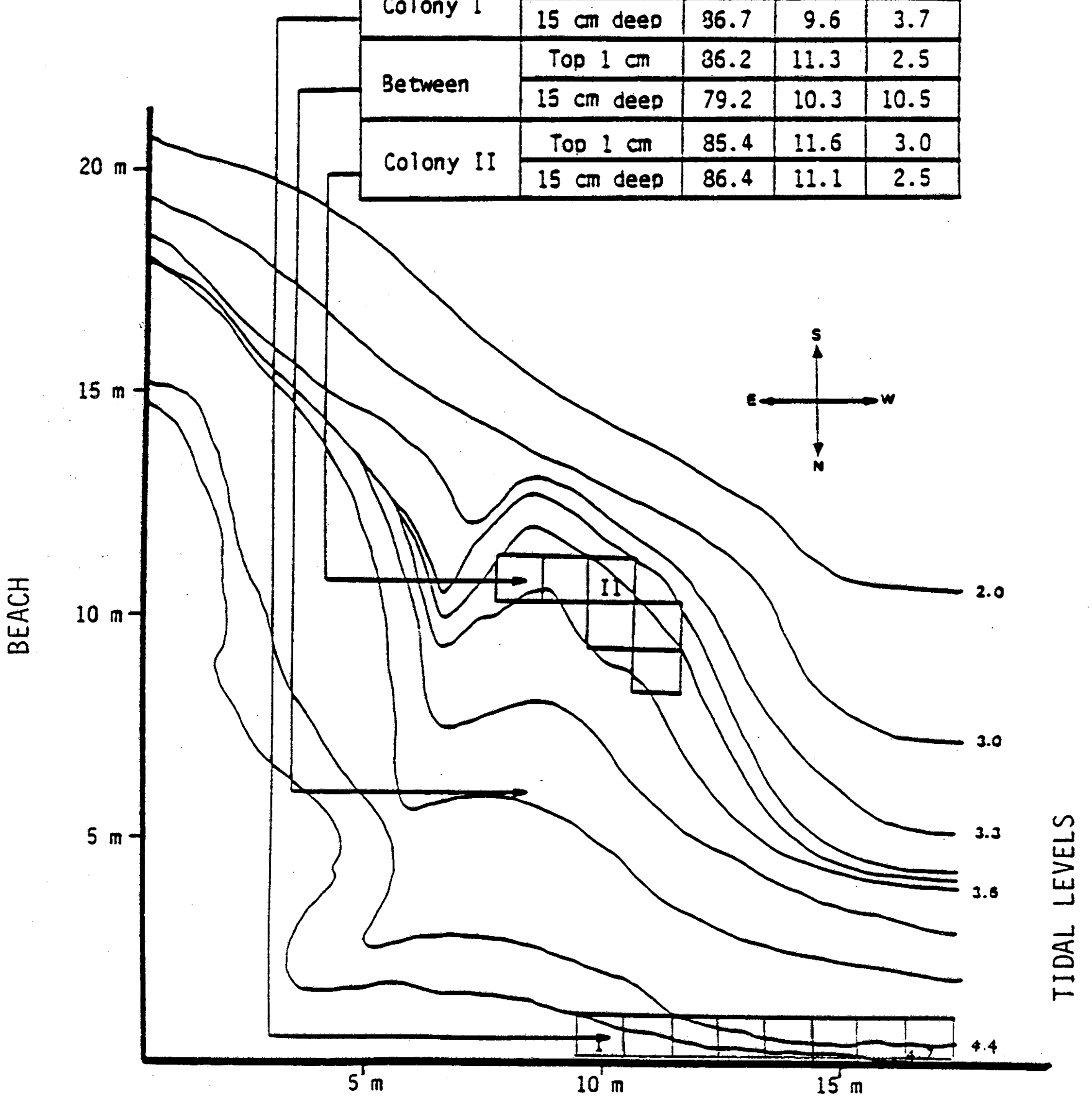
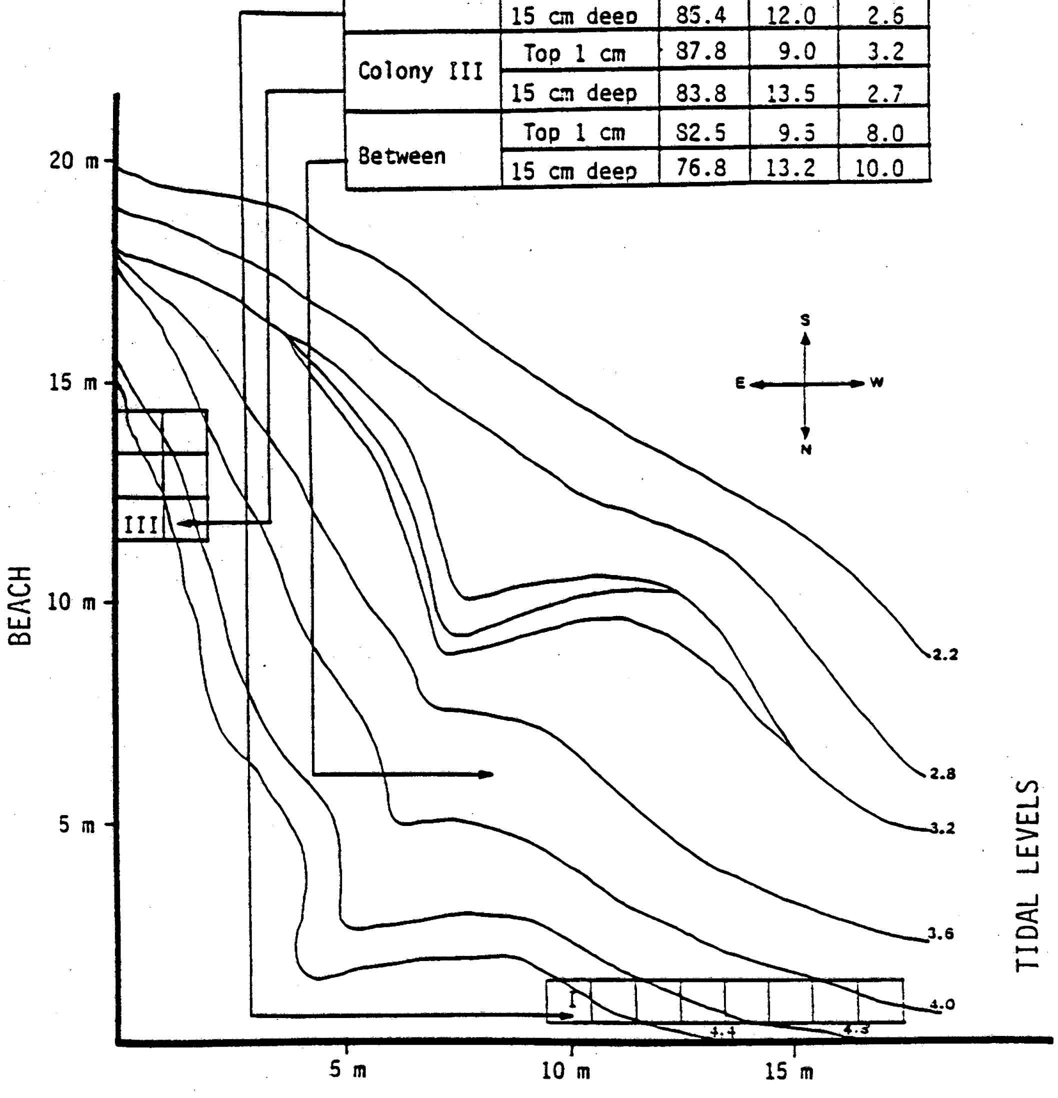


Figure 7. Soil texture analysis for the permanent and temporary burrow locations in 1982. Permanent and breeding burrows are located in colonies I and III while the temporary burrows are found between these areas.

SOIL TEXTURE ANALYSIS, 1982
(samples 100 gm)

Sample Location		% Sand	% Clay	% Silt
Colony I	Top 1 cm	82.8	10.7	6.5
	15 cm deep	85.4	12.0	2.6
Colony III	Top 1 cm	87.8	9.0	3.2
	15 cm deep	83.8	13.5	2.7
Between	Top 1 cm	82.5	9.5	8.0
	15 cm deep	76.8	13.2	10.0



POPULATION CHARACTERISTICS

Topographical Distribution

The study site contains two distinct populations--a permanent and a transient population.

Permanent Population

This group builds permanent burrows which remain in the same location for the entire year. A density variation, depending upon the season, is the only change occurring in this population. The adult males of this population show a preference for the higher shore level (4.0 feet tide level) for the construction of their burrow sites. The results obtained during the summer of 1982 for colony III (Fig. 9) show the colony localized at the highest level with a population distribution of 85.3% adult, 13.9% medium and 0.8% small male crabs. In colonies below the 3.8 feet tide level there are fewer adults and more medium to smaller sized crabs (75.5% adults, 23.1% medium and 1.4% small males). This distinct preference of adult males for the highest sites on the shore has also been reported for *Uca pugilator* (Christy, 1980). This preference for specific localization by adult males has consequences in male and female interactions during the mating season.

Transient Population

This group has a seasonal behavior. The distribution and density of this population depends on the temperature, substrate moisture and ecological changes. The preference by adult males for specific sites is not observed in this population, and there are no courting males in this population during the breeding season.

The distribution of the two populations for 1981 and 1982 is shown in Figs. 8 and 9. The permanent population is located at higher elevations on the beach, at tide levels of 4.0 feet and above, while the transient population covers the portion of the beach below the 4.0 feet tide level.

Density

The density and the male/female ratio varies greatly, depending on the season.

The surface density of the permanent population shows a significant increase during June, July and August while the surface density decreases in the winter due mainly to hibernation (Fig. 10).

The change in density of the transient population is observed at two different levels: 1. The population distribution is seasonally dependent. During the winter the transient population resides between the 2.0 and 4.0 feet tide level, an area that is outside the permanent population resident area. During the breeding season, the bulk of the

Figure 8. Map of the study site in 1981. The *Uca crenulata* population is distributed from tide levels 4.7 to 2.0. The mating colonies are located in areas I, II and III during the breeding season.

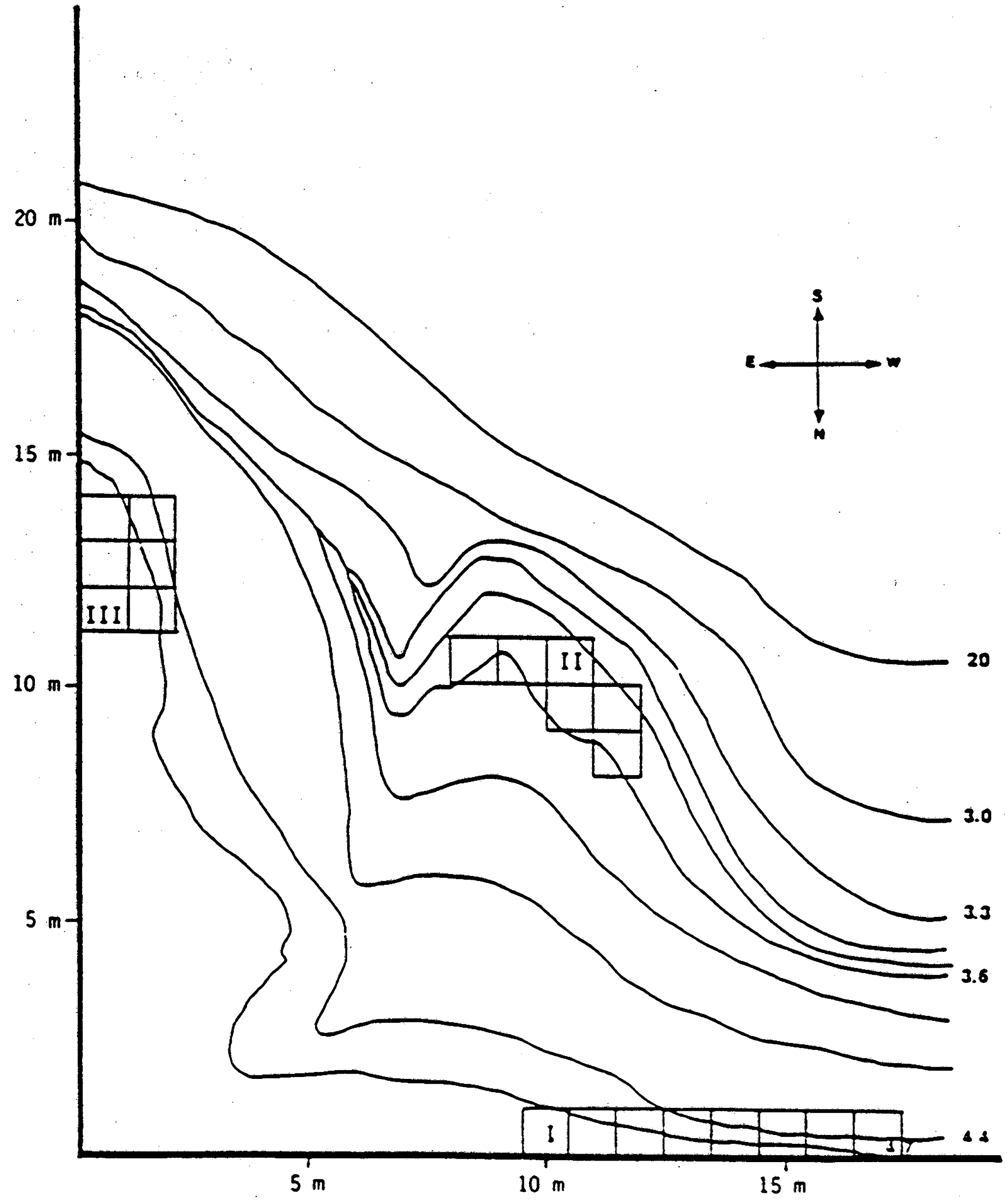

S
E
W
N
20 m
15 m
10 m
5 m
5 m
10 m
15 m
III
II
I
20
3.0
3.3
3.6
4.4
3.7

Figure 9. Map of study site in 1982. The *Uca crenulata* population is distributed from tide levels 4.4 to 2.2. The mating colonies are located in areas I and III during the breeding season. The temporary colony is located between area I and III and the water edge.

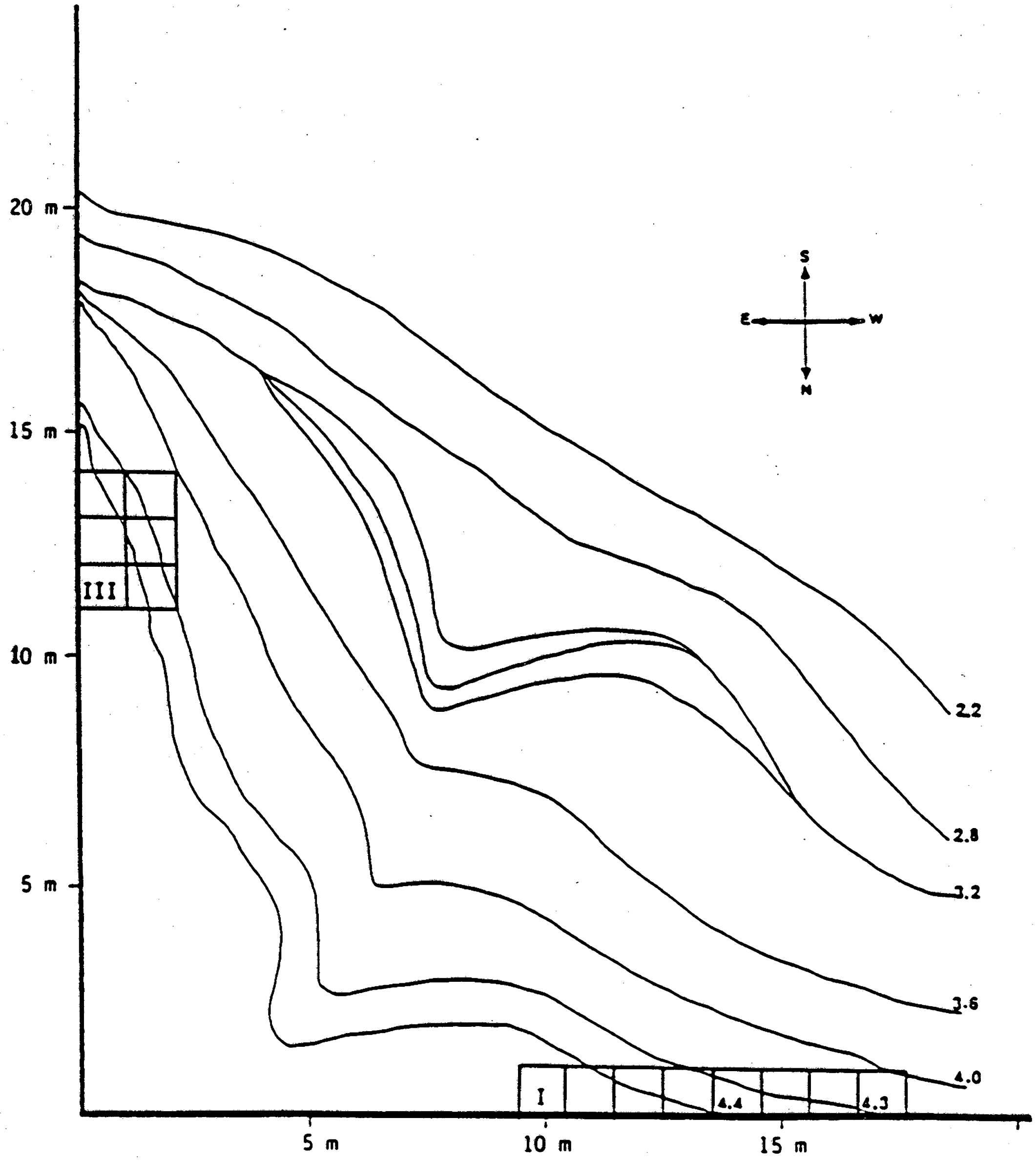
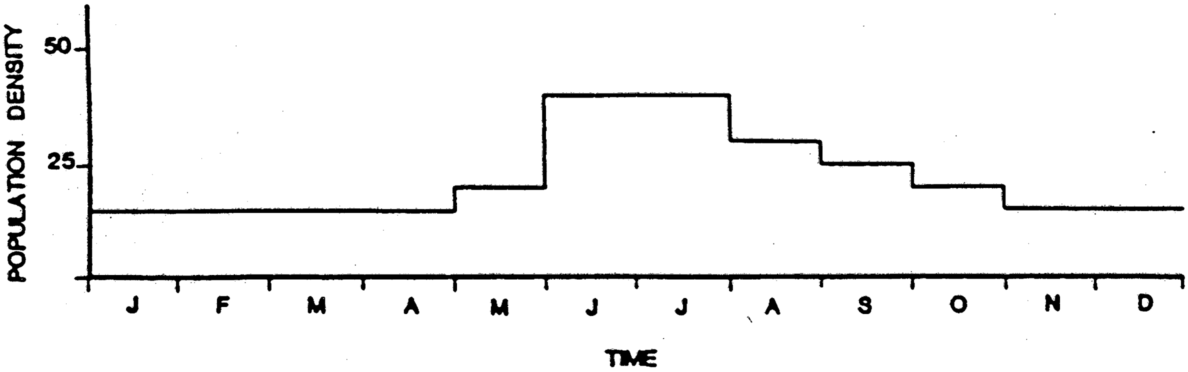

20 m
15 m
10 m
5 m
5 m
10 m
15 m
S
E
W
N
III
I
2.2
2.8
3.2
3.6
4.0
4.4
4.3

Figure 10. Population density of colony I showing the number of crabs/m^2 during 1982.

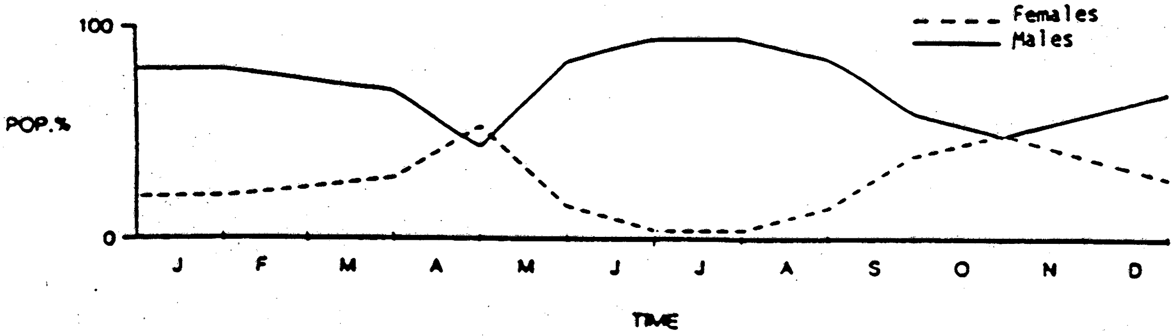

POPULATION DENSITY
50
25
J
F
M
A
M
J
J
A
S
O
N
D
TIME

transient population is found in feeding aggregations, which are located at the water's edge during the low tide period. Here, the density of the transient crabs is five times higher than around the burrow area, as the transient colony is packed on a narrower strip of land. 2. The surface density of crabs doubles during the warmer months of the year (26 to 49 per square meter during the breeding season). This increase in surface density contributes to the mating activity, as the abundance of females on the surface provides greater contact between wandering females and mating males.

Male and Female Ratio

In the permanent colony, the proportion of males to females on the surface is higher in the summer than during other seasons (Fig. 11). The male/female ratio is the same before the mating period in April, as it is at the end of October (50/50). During the breeding season on the other hand, 90% of active animals are males. This difference can be explained by the fact that most of the fertilized females are underground in breeding chambers. As the mating season ends, the females return to the surface and join the males in feeding behavior and burrow construction.

The male/female ratio in the transient population is quite different. The high number of males forming the transient population during the winter (72%) decreases in


Females
Males
100
0
POP.%
J
F
M
A
M
J
J
A
S
O
N
D
TIME

the summer when the majority of the dark crabs are females (67%). The seasonal variation of females on the surface, 28% in winter and 67% in summer, can be explained by assuming that the females spend more time in hibernation. Dark males do not display typical mating behavior, so their presence during the mating season does not affect the normal mating behavior.

The conditions required for a maximum success in male/female interaction for breeding and continuation of the species are met when you consider that the greatest density of mating males in the permanent colony coincides with the increased activity of females on the surface during the breeding season.

BEHAVIORAL ACTIVITIES

Introduction

The activities of fiddler crabs can be divided into three main categories: maintenance, defense, and social activity (Crane, 1975). Social activity throughout the genus is largely confined to the daytime and more specifically to several hours around low tide. As the water begins to ebb and animals emerge from their burrows, the initial activity of the animals is feeding. Then, as the soil dries burrow repair and excavation begins, replacing some of the feeding activities. An hour or two into the ebb tide period waving activity begins and, in some species, attains peak activity one hour before low water. In others, the waving activity is most active shortly after the tide turns. Intermale combat appears to peak an hour earlier than the waving display for any one species, but virtually vanishes within an hour after low tide. Neither combat nor threat behavior has been reported at night.

This brief description of Uca behavior given by Crane (1975) concerning the fiddler crabs of the world is a valuable reference from which to compare the behavior observations made on the species U. crenulata.

Environmental Influence on Behavioral Activities

In 1973, Honegger made the first observations of the

Uca crenulata population living in the Aqua Hedionda lagoon in Carlsbad. He attempted to determine the impact of tidal rhythm and light-dark cycles on the crabs' rhythmic motor activity. The experiment was conducted in the laboratory under artificial light and tide conditions controlled in a manner that separated the influence of these two factors. Honneger (1973, (1) (2)) indicates that Uca crenulata has an endogenous rhythm (24.8 h) with a period close to the tidal cycle, which may be synchronized by light as well as by tidal cues. The display of this endogenous rhythm, however, is poor.

In 1981-1982, I made field observations for this study in the same location studied by Honegger seven years earlier, the "Aqua Hedionda" lagoon. The different behavioral activities studied were divided into six categories: feeding, waving, fighting, burrow building, burrow sitting and surface inactivity. The frequency or existence of these different displays depends upon seasonal and environmental factors such as weather, temperature, light and tide level. The behavioral activities vary with yearly as well as daily environmental changes.

Daily Changes

The observation and data acquisition was primarily done during the daylight low tide periods. The study area was divided and marked into square meters. During each study session specific square meters were selected and all the animals in that area were observed and their activity categorized every 15 minutes. From this data the location and duration of each activity in the crab's normal low tide cycle was determined.

The predominant initial activity in both summer and winter is feeding (Fig. 12). In summer the first three hours are predominantly eating while the last two hours are dominated by waving activity. Burrow building and fighting which each occupy about 10% of the first two hours are of minor importance as waving activity becomes predominant. Category "Immobile" represents a lack of activity rather than a specific direction of activity. This aspect is common in the summer cycle and is not observed in winter animals. In winter the animals return to their burrow as soon as feeding is accomplished (Table 1 in index).

The density of animals above ground in the winter is about 50% of the summer density if the weather is warm. Figures 13 and 14 relate activities of the crabs to the seasonal ebb and flow of the tide. The sequence of the activities are directly related to this external influence. The number of animals and intensity of activity however is related to the ambient temperature.

Waving behavior is one activity that is temperature dependent. As the summer temperature drops below the

Figure 12. Behavioral activities of the crab colony during 1982. Each graph covers the entire low tide period and shows the percentage of crabs displaying during each hour of observation. E: eating, W: waving, IB: in burrow, I: immobile, BB: burrow building, and F: fighting.

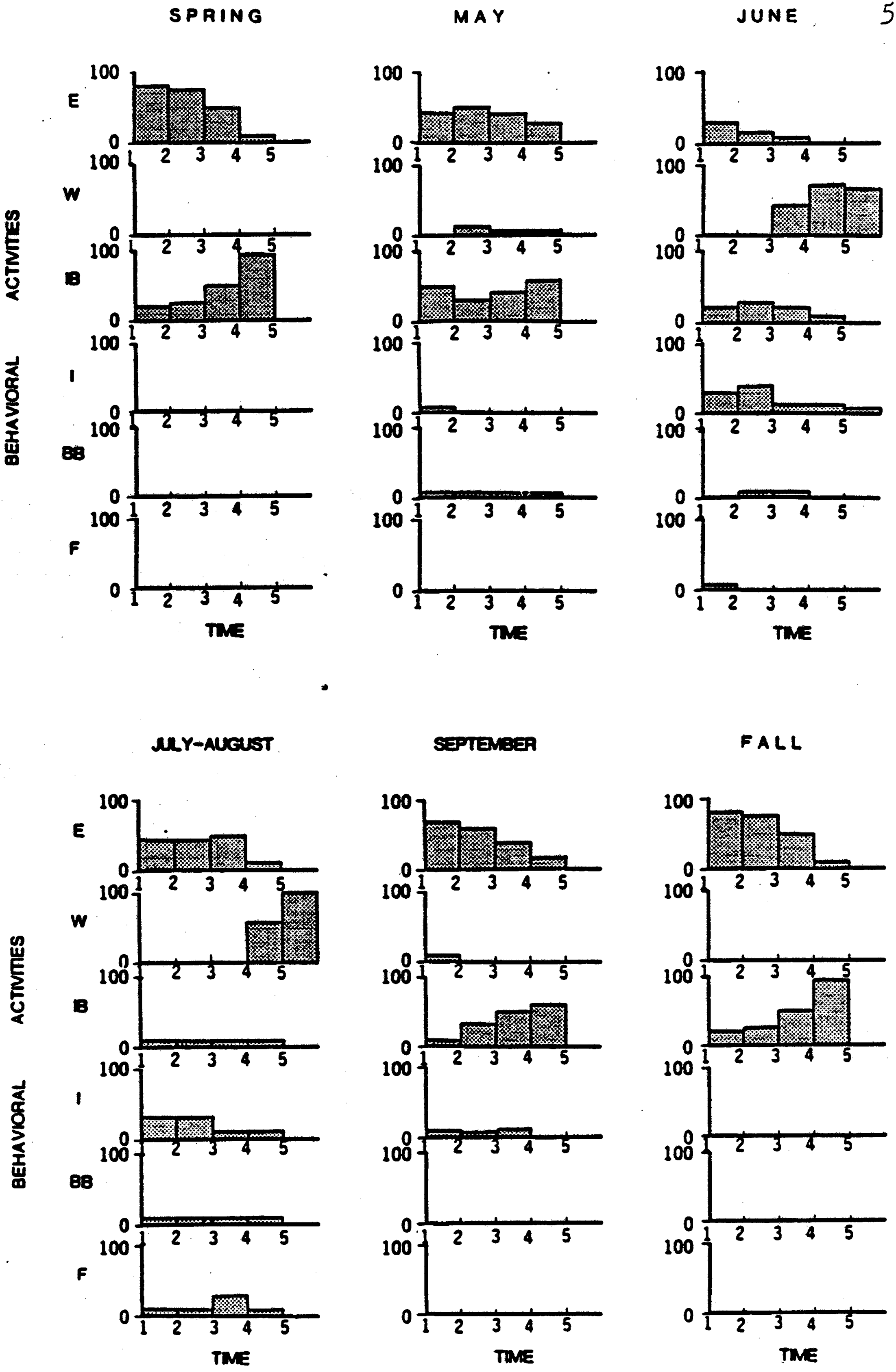

SPRING
MAY
JUNE
JULY-AUGUST
SEPTEMBER
FALL
BEHAVIORAL ACTIVITIES
E
W
IB
I
BB
F
100
0
1
2
3
4
5
TIME

Figure 14. Behavioral activities in the winter. The observation period takes place in colony I during the low tide. The air temperature is measured every hour and can be an important environmental factor influencing the crabs' activities. In this specific case, December 9, 1981, the decrease in range of behavioral activities is observed in the winter: E: eating, F: fighting, IB: in burrow. H.H.: high high tide, H.L.: high low tide, L.L.: low low tide, L.H.: low high tide.

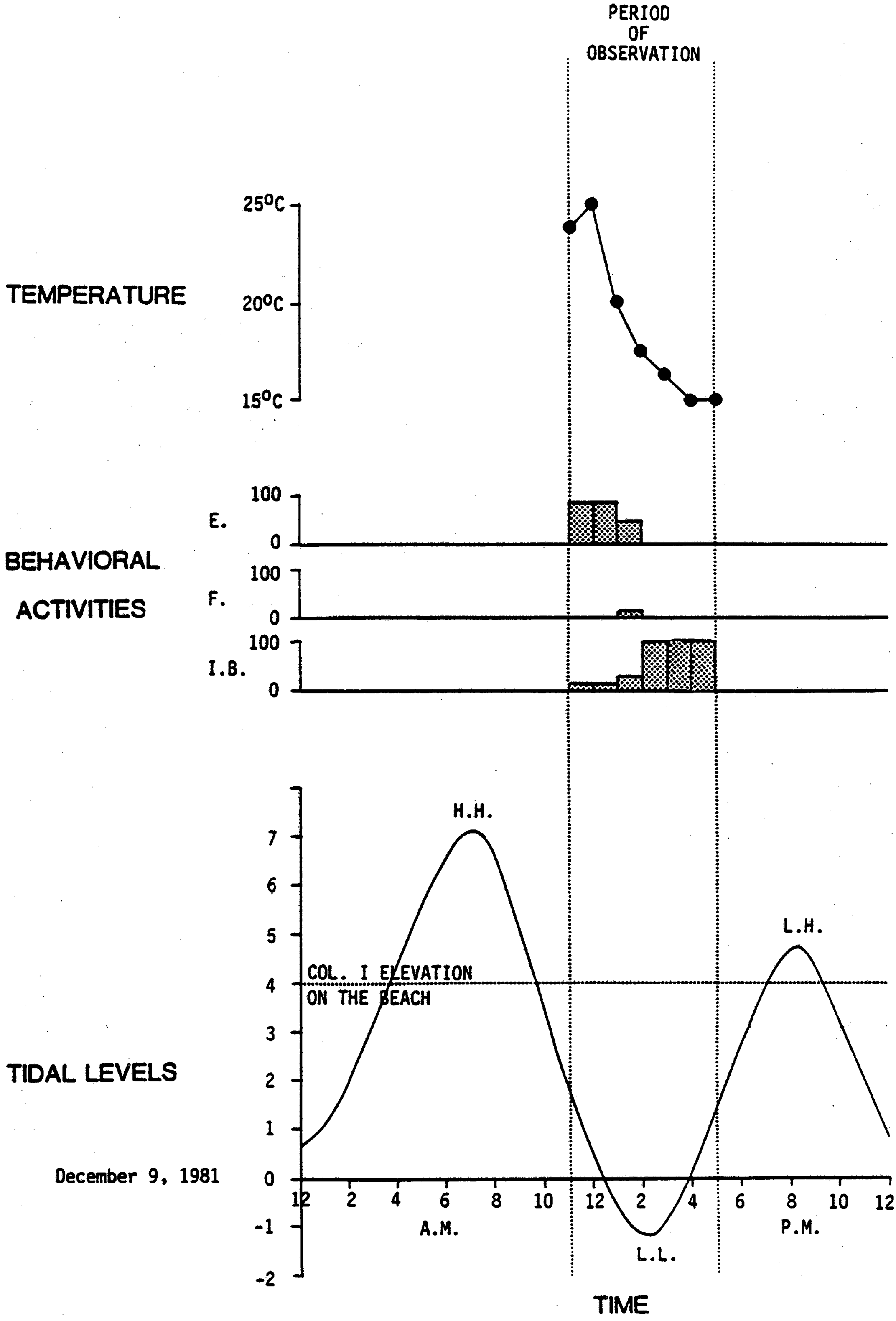

PERIOD
OF
OBSERVATION
TEMPERATURE
25°C
20°C
15°C
BEHAVIORAL
ACTIVITIES
E.
F.
I.B.
100
0
TIDAL LEVELS
December 9, 1981
7
6
5
4
3
2
1
0
-1
-2
H.H.
L.H.
L.L.
COL. I ELEVATION
ON THE BEACH
12
2
4
6
8
10
A.M.
P.M.
TIME

Figure 13. Behavioral activities in the summer. The observation of the crab population located in colony I takes place during the low tide period. The air temperature is measured every hour because any variation in this environmental factor can influence the crab activity on the surface The full range of activities is observed in the summer. W: waving, I: immobile, BB: burrow building, E: eating, F: fighting and IB: in burrow. H.H.: high high tide, L.H.: low high tide, L.L.: low low tide, H.L.: high low tide.

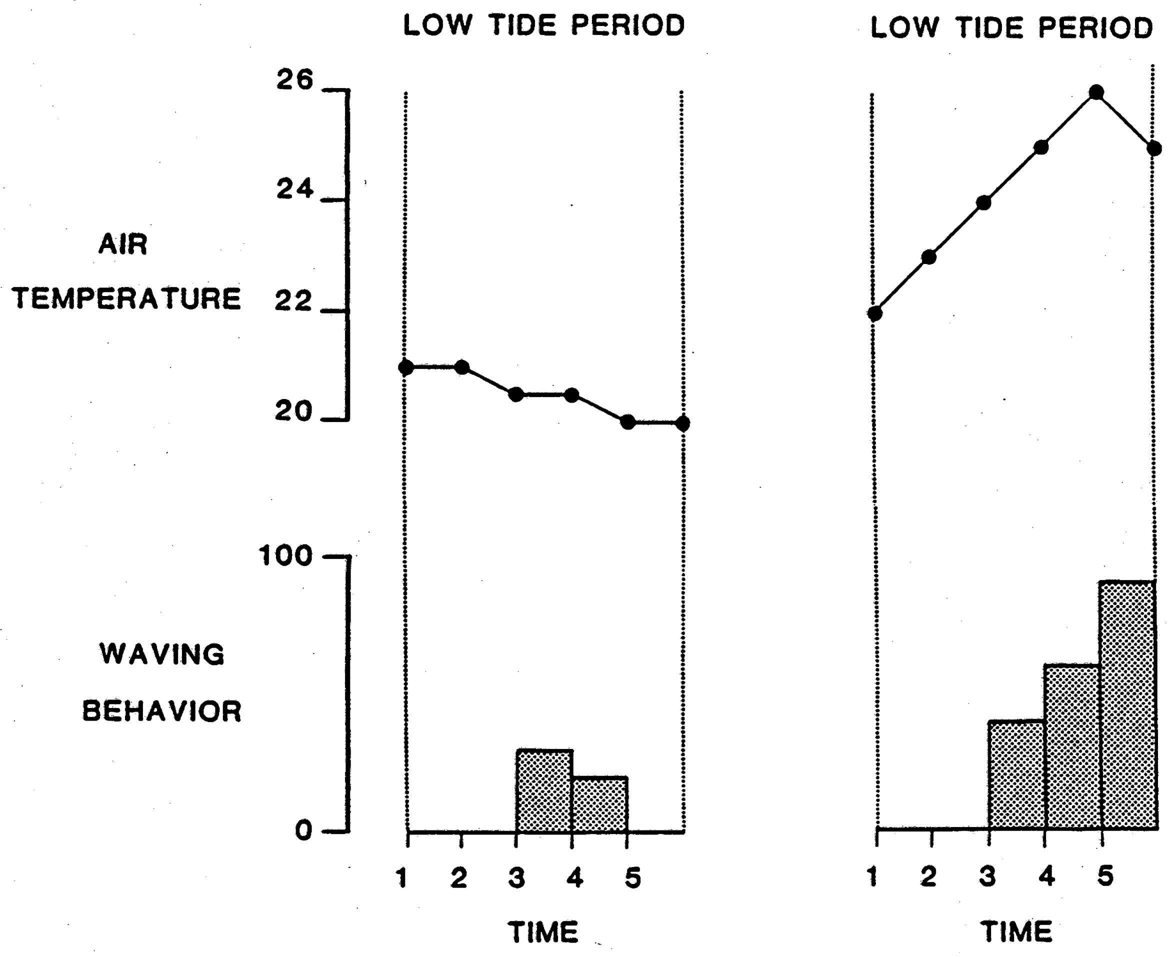
optimum of 30°C, waving activity decreases, until at 20°C, the waving ceases. Waving activity is sensitive to temperature variations within a single day. When optimum low tide is in the cooler portion of the day, waving activity is minimal. Waving activity is at an optimum (Fig. 15) when the tide ebbs during the hotter afternoons.

During the winter, the tidal rhythm has the same regulating role, but because of the different physiological needs, the range of activities is reduced. Waving behavior is non-existent and the absence of breeding burrows and competition for females reduces the male's aggressiveness. As the tide recedes, crabs emerge from their burrows to feed. Two or three hours after the beginning of ebb tide, the number involved in feeding decreases and males as well as females return to their burrows (Fig. 14). Some crabs seal their burrows, depending on the temperature and level of the next tide. Fights and activities other than "eating" or "in burrow" are rare. Cold weather (10-12°C) decreases the number of individuals feeding on the surface as well as the feeding time. If the population of crabs has had a good opportunity to feed, the majority of crabs will stay in their burrows during the next several low tides occurring in cold weather.

Yearly Changes

The cold months are characterized by long below-ground

Figure 15. Influence of temperature on the percentage of waving activity displayed by the mating males.


LOW TIDE PERIOD
LOW TIDE PERIOD
AIR TEMPERATURE
26
24
22
20
WAVING BEHAVIOR
100
0
1
2
3
4
5
TIME
1
2
3
4
5
TIME

inactivity followed by unusually long periods of feeding and passive sitting or wandering. As the weather warms and the mating season approaches (May), waving behavior and aggressiveness appear as well as an increase in burrow building. Once the mating season is complete, breeding season behaviors vanish and below-ground inactivity predominates (Fig. 12).

The number of males and females observed in the permanent colony varies with the time of the year. In winter and spring the population density of females represents 20 to 50% of the total population. In summer, on the other hand, many females are gravid and below the surface and as non-gravid females spend only small amounts of time in the mating colony, most of their behavioral activities take place outside of the mating colony. For this reason animals observed in the mating colony during the summer reflect predominantly the male population.

Figure 12 gives an overview of the behavioral pattern for the year 1982. The year is divided into three sections: spring, breeding season, and fall. A seasonal variation in range, timing and interrelation of activities can be observed.

The two predominant activities present during the non-breeding season are "eating" and "in burrow" and these show an inverse relationship. The other activities such as burrow building, fighting, immobile at the surface, occur rarely and are not significant while the waving behavior is non-existent. As the breeding season approaches (May), an increase in burrow building and a sudden appearance of low frequency waving is observed.

The breeding season (June, July and August) is characterized by a larger range of activities with a marked dominance of the waving behavior. "Eating" as well as "in burrow" behaviors are present all year but the percentage of time spent performing these activities decreases during the breeding season. The opposite observation can be made with aggressive behavior: While non-breeding crabs show very little aggression, breeding males and females compete strongly for burrows during the summer, giving rise to complex aggressive behaviors. Burrow building is also important to the mating male and is characteristic of the breeding season. In summer, eating, fighting and waving behavior can be interrupted by long periods of immobility or sunning.

During the breeding season, eating, waving and aggressive behaviors are observed at night but at a much lower frequency. Weather conditions such as nocturnal fog make detailed observations difficult. The observations of behavioral activities of _U_. _crenulata_ at night differ from the general description given by Crane (1975).

The final breeding cycle of the summer ends by the 31st of August and accounts for the sudden change in behavioral activities. This is coincident with a marked decrease in "waving" and "immobile" behavior as well as "burrow building" activities. The rise of "eating" and "in burrow behavior" characterizes the beginning of a new non-breeding period (Fig. 12).

A population of crabs raised in the laboratory beginning in October 1981 was maintained at constant L/D cycles all year. In the spring of 1982, the males of the lab colony displayed waving behavior during the same week that crabs inhabiting the lagoon began waving. This waving display, in the absence of any environmental stimulus suggests the strong endogenous character of _U_. _crenulata's_ mating behavior.

Burrow Building Behavior

Introduction

The burrow building behavior in _Uca_ _crenulata_ is a complex activity. The females, males and juveniles display distinctly different behaviors. Building can be observed under the surface, at the burrow mouth, as well as around the burrow's entrance, depending on the crab's sex, age and environmental factors, such as season, temperature and tidal levels.

Crane (1941) mentions that species that build burrows on "yielding" mud have the shallowest holes while species on relatively dry "mud sand" beaches, or along the banks of drying streams dig the deepest burrows. The burrows of individuals within the same species vary considerably depending on location and size of the crab. The instinct of burrow-making appears least developed in certain species such as _U. panamensis_ which lives on stone-strewn beaches. Most _Uca_ have relatively simple burrows in which the main chamber proceeds diagonally downward. Regardless of the direction or depth of the digging, the method employed is the same. The crab digs with the legs of the minor side. This side precedes the crab into the hole and curves around the excavated mass, forming a basket-like structure used in removing the ball of soil. All material from the burrow is carried a short distance from the entrance and either deposited on the spot, or more rarely tossed. The soil balls removed from the burrows are always many times (10X) larger than the feeding pellet, and are often well compressed. Young crabs of all species do not dig, but run freely in and out of the burrows built by adults, both of their own and related species. The adults pay no attention to the juvenile animals. The first burrows of the juveniles are shallow and close to the low-tide level while the larger displaying crabs select burrows that are typically near the high tide mark.

A few species of _Uca_ (Crane, 1975) may construct some type of structure near or around their burrow entrance. The structures may take the form of a wall surrounding the burrow mouth and have been termed chimneys or pillars. In more elaborate developments of the pillar, a symmetrical and smoothly arched hood is formed, which is always concave on the side closest to the burrow.

The significance of these different constructions have been speculated upon by several authors, but no experimental data has been collected to verify any of their hypotheses. Nadia Zucker, in a 1974 publication concerning the fiddler crabs, Uca terpsichores, presents evidence suggesting that the "shelters" or "hoods" of U. terpsichores decrease territory size by allowing high population densities to exist without the expected increase of aggression between neighbors. The usual territory is a 360° circle around the burrow with a radius of up to 7 cm. The close proximity of male burrows or the occasional presence of hoods and shelters limits the display to 180° in front of the shelter opening. The shelters are destroyed by the incoming tide and new ones may be erected the following day.

Christy (1980) describes in detail burrow construction in the species U. pugilator. He shows the existence of two types of burrows: the temporary burrow and the breeding burrow. Using plaster to make casts he was able to make measurements and construct models of the burrow. The breeding burrow contained chambers with a descent angle of 41°

and a chamber depth of 43 cm as compared to 79° angle and a depth of 20 cm in the temporary burrow. Their structural differences reflects a functional difference.

Importance of the Burrow in the Life and Mating Success of Uca crenulata

For the *Uca crenulata* population in general, the burrow is important as a shelter during the high tide. If the crabs are not protected underground, they would be redistributed during each incoming and receding tide. The burrow also has its importance during seasonal changes in providing a place for hibernation, protection against predators and dessication during hot periods and low tides.

It is during the mating season that one can best observe how much the crabs' activities are centered around and dependent upon the burrows, showing the burrows' fundamental role in the crabs' social behavior. The male establishes his territory around the burrow by fighting and displaying antagonistic behavior against any intruder. His courtship behavior, as well as his mating success, depends on the establishment and ownership of a burrow. The waving display takes place at the burrow entrance, and if the female is receptive to the male, she follows him into his burrow. If the burrow construction fits her requirements she remains inside for mating and incubation of the eggs.

The existence of three types of burrows with different purposes and inhabitants shows its importance in the *Uca* *crenulata's* social life.

Types of burrows. Christy (1980) mentions the existence of two types of burrows in the *Uca pugilator* population. However, field observations of *Uca crenulata* suggest the existence of three types of burrows as delineated by their structure as well as purpose.

Temporary burrow. The temporary burrow is used only during high tides by crabs lacking mating behavior. These temporary burrows associated with the wandering population, can be found only during the mating season. They are located on the shore outside the mating colony, they are shallow and do not contain chambers.

Permanent burrow. The permanent burrow is used during the non-mating season by the total crab population. This burrow not only protects the crab during high tide but is also the center of his activities. The crab builds and maintains the burrow, protects it against intruders and feeds around it. This burrow does not appear to have many chambers but is deeper than the temporary burrow. It is usually found on the highest elevation of the shore inhabited by the crab population. In the mating season this area becomes the breeding burrow location.

Breeding burrow. These burrows form the mating colony and are used by the mating males and females. They possess chambers and may be as deep as 45 cm.

The behavior of males and females in relation to these burrows, their construction, defense and occupancy will be discussed separately for each sex.

Male behavior. The breeding burrow is critical for male courtship display as well as his mating success. The high population density of crabs, characteristic of a mating colony leads to a decrease in the distance between burrow entrances, to as low as 2 cm in some cases. This close proximity induces intense territorial fighting. The burrow mouth is at the center of a 5-7 cm territory which is defended 24 hours a day by the male. Burrow construction, so important to the mating season, takes place mainly after the tide recedes from the burrow entrance. The crab emerges from his burrow carrying sand balls 0.5 to 0.75 cm in diameter in his ambulatory legs. He deposits these balls around the burrow entrance or carries them as far away as 10 cm. Occasionally, crabs may push these balls into neighboring burrows. When the burrow is repaired or additions completed, the male then joins the other males in feeding or begins his waving behavior. Males as well as females take part in burrow construction but their behavior and timing is different. Males build breeding chambers and work in their burrow immediately after the water recedes from the entrance, while female activity is most pronounced when the tide returns to cover the burrow sites.

Female behavior. Female behavior depends on whether she is gravid or non-gravid.

Non-gravid females. The non-gravid females spend the first three to four hours of low tide in feeding aggregations along the water's edge. One to two hours before high tide they begin to move back up the beach through one or more of the mating colonies.

If the female is ready for mating, she responds to the waving display of the males by checking the burrow entrance, at which time she may enter and remain in the burrow. The majority of the time, however, she re-emerges and checks neighboring burrows. Females have been observed to check up to 60 burrows without making a selection.

If they are not interested in males, they choose a burrow existing outside of the mating colony. They then prepare the burrow and spend more time eating, or they may enter early and seal the entrance. Occasionally, they may check empty burrows within the mating colony. Once the chosen burrow is rebuilt to their liking, they behave as they do if burrow selection is outside of the mating colony.

Gravid females. Gravid females utilize breeding chambers from 1 cm to 40 cm below the surface. Most gravid females stay in the breeding chambers from the time of fertilization until the larvae are released. Nevertheless, some gravid females (3%) are observed on the mating colony surface. They do their burrow building early in the low tide period, close their burrow, and are under the sand when the tide comes up. These gravid females are usually found only a few cm below the surface.

The females, gravid or not, use the same technique as the males for burrow building, using their ambulatory legs to remove the sand balls from the burrow.

The described burrow building behavior takes place during the mating season. The differences between male and female building behavior does not exist during the non-mating season, when permanent burrows are built. At that time, males as well as females, rebuild and repair their burrows first as the tide goes out and then feed around their burrow's entrance until the tide returns.

Construction Activities Other Than Burrow Repair

Some of the constructions described by Crane (1975, 1941) can be seen in the species *U. crenulata*.

"Chimneys" and "hoods" are observed sporadically in the permanent or mating colony. The owners of the few burrows (10%) decorated by these constructions are always males.

While "hoods" were observed only during the mating season in the mating colony, chimney formations can be seen all year around. Hood building is also observed in the laboratory colony. The value of these structures is undetermined. The low percentage of burrows with such formations and their appearance without obvious relation to behavioral or ecological factors are difficult to explain. The "hood" which is observed only during the mating season could have some importance in the female burrow choice (one out of the only four burrows observed to be chosen by females, in response to male waving, displayed a "hood").

Plugging behavior is common with both males and females. During the non-mating season, the crabs forming the permanent population may close their burrow early in the tidal cycle. Field observations show that when plugging occurs it follows a particular pattern: Thirty minutes after the receding tide 25% of the burrows are plugged; after 1 hour, 90% of the burrows are plugged, and after 1½ hours, 100% of the burrows are plugged. The factors triggering this behavior are not clear but appear to be related to temperature and an unusually high tide. Crabs of all ages and sex behave this way during the non-mating season. During the mating season, this behavior is observed in the temporary colony an hour before the next high tide or during an exceptionally cold day. All of the gravid females upon finding their own burrows in the mating colony plug their burrow irrespective of tide or weather. No mating male is observed plugging his burrow, unless a female has responded to his waving display and has entered his burrow.

When comparing the different cases of burrow plugging, one can observe two triggers for this behavior: reproducgive instinct and adverse environmental factors.

Feeding Behavior

Introduction

The ability of an organism to find nutrition in his environment is one of the basic conditions for his survival, and continuation of his species. Food resource is then a major factor governing animal distribution.

Feeding Mechanism in Uca

During low tide, the crab sits on the shore with the buccal area almost vertical. In this position the fiddler crab scrapes a bit of substrate in a small cheliped and places it between the inner edges of the third and second maxillipeds, which are held ajar during feeding (Crane, 1975).

Among the mineral particles scooped up are detritus, algae, bacteria and perhaps nematodes. Within the buccal cavity, the food material is selected for ingestion and then passed on to the mouth. Unsuitable material, mainly large organic particles, is passed on to the bottom of the buccal cavity and permitted to fall out between the third maxilliped.

Two processes are involved in the feeding mechanism: coordinated action of the mouth parts and a flotation process which utilizes water from the gill cavities. The importance of the mouth parts in the substrate particles separation as well as the importance of water for the flotation process is described in detail by different authors (Altevogt, 1957; Pearse, 1912; Miller, 1961).

Species-specific modification of the mouth parts in relation with substrate consistency. Different species of *Uca* feed on different types of substrate and Miller (1961) observed some anatomical differences depending upon the type of substrate fed on. The sand grains on the beaches inhabited by *U. pugilator* contain some detritus and nematodes but most of the organic material is comprised of bacteria and algae. This crab appears to ingest a minimal amount of sand and the food must therefore be separated from the mineral fraction. This cleaning process is facilitated by the presence of a large number of spoon-tipped hairs located on the second maxilliped. In the case of the marsh-inhabiting *U. pugnax*, food is more readily available because the silt with which it is generally associated is of sufficiently fine texture to enable it to be ingested (no complex cleaning process is required).

Males and females feeding behavior. Males use the single minor cheliped, apparently at a faster rate than the female uses her two chelipeds which she uses alternately. Sometimes single scrapes are made, sometimes four or more at a time, before the material is carried to the mouth. This does not appear to be a species difference; the number of scrapes is probably related to the character of the terrain and the type of food.

Uca crenulata's Feeding Behavior and Feeding Mechanism

Male and female feeding behavior. Uca crenulata's feeding behavior was observed in the field and comparison made between males and females in both temporary, permanent and breeding populations.

Males. Males from breeding and permanent colonies feed around their burrows. Mating males begin eating as the tide goes out and pursue this activity for three to four hours. They shift then to the courtship behavior as the female feeding aggregations return up the beach. In winter males from the permanent colony begin to eat as the tide goes out, however they eat for 2 to 3 hours, depending on the weather conditions. Less time is spent on the surface in cold weather. Hibernation may overrule the pattern described above. In December, for instance, most of the crabs remain inside their burrow and very little feeding behavior is observed, even when the weather is warm.

The time spent feeding by the temporary male population depends on the weather conditions. If the weather is cold and the sand remains wet they remain around their burrow longer than if the sand dries fast. When they do leave their burrow, they form feeding aggregations along the water's edge. These aggregations begin the return trip up the beach four hours after the beginning of the ebb tide.

Females. Mating season. Non-gravid (NG) females feed in feeding aggregations for 3 to 4 hours before moving up the beach looking for burrows. Gravid (G) females usually feed within the mating colony and eat for shorter periods than females of the feeding aggregation.

Non-mating season. Females eat in the area surrounding their burrows for a few hours, before returning to the burrow. Their feeding behavior is similar to the males' during the non-mating season.

In summary, the diurnal feeding activity takes place as the tide ebbs and lasts for two to four hours depending upon weather conditions, tidal patterns or population stage (temporary, breeding, or permanent population). Nocturnal observations did not provide sufficient data to give a detailed description of nocturnal feeding behavior.

Feeding mechanism and sand ball formation. Variations in sand ball formation in males or females. The feeding behavior of males and females is different, not only in timing relation to tidal pattern but also in the number and formation of the food pellet or the so-called feeding sand ball. Measurements made in the field show that a female scoops an average of 8 ± 2 before carrying the sand to the buccal area and releasing a sand ball, while the male scoops an average of 9 ± 2 to produce a sand ball. The number of scoops necessary to form a food pellet varies with the individual and depends on the substrate location and composition. Under normal conditions, when the crab scoops particles of sand he scoops an average of 8.9 times before the appearance of a sand ball (Crane, 1975). When the crab feeds on algae, where no sand particles are, he requires as many as 28 scoops before releasing a pellet. The number of feeding balls released per minute is the same for males and females (5/min.) in *U. crenulata*.

Females use both of their small chelae to feed while the male has only one small chela with which to perform this activity. The observation made by Crane (1975) that male fiddler crabs use their cheliped at a faster rate than females would apply to the *crenulata* species only if she means that the number of scoops made by a male per minute is higher than in the case of a female (9 ± 2 vs. 8 ± 2). If, on the contrary, she refers to feeding balls produced per minute there is no major difference between sexes in the case of *crenulata*.

Special feeding mechanism used in the case of a male with two major chela. A few males of the colony possess two major chelipeds instead of one. This physical abnormality can affect much of their behavioral activities. Crane (1975) mentions that when a male loses the minor cheliped, he attempts to use the major in feeding. If the degree of hypertrophy is not too great, he may successfully support himself for weeks or months until regeneration is accomplished. Crabs having two major chelipeds bring the buccal region in contact with the substrate, a method which permits the animal to survive (Crane, 1975). Two of these handicapped crabs were observed during the mating season in the feeding aggregation and one was found hibernating. The three individuals carrying this abnormality had reached the adult stage so whatever feeding method used was apparently successful.

Water presence required for feeding behavior. The presence of wet substrate for feeding behavior is necessary in *U. crenulata* and can be induced by sprinkling salt water on the sand before sprinkling food particles.

In the field, feeding behavior always takes place as the tide goes out, while the substrate is still wet. As the substrate dries the crabs turn to other activities.

Variation in feeding behavior in relation with burrow types. Signs of feeding behavior are observed on the beach by lines of pellets radiating from the burrows' entrance. The crab moves steadily forward as it feeds, whether it is a permanent burrow resident or a wanderer.

When feeding around the burrow, some fiddler crabs retreat down their burrows periodically (Smith and Miller, 1973). This provides access to water and moist soil and prevents them from leaving the burrow site for less drained substrate as does *U. pugilator*. This behavior is observed in portions of the Uca crenulata population and shows how variation of feeding location of the crab corresponds to his burrow type:

--Permanent and breeding burrows are deep as well as complex in architecture. They retain a small amount of sea water even when the tide has ebbed. This permanent source of water prevents dessication and allows the burrow's owner to remain around the burrow for many hours during the mating season. A few minutes down the burrow are sufficient to moisten his gills and feeding structures.

--The temporary burrows on the other hand are shallow, do not possess chambers and are less adapted for water retention. The owner of this type of burrow is a dark crab (male or female) which leaves its burrow soon after ebb tide and forms feeding aggregations at the water's edge or on less drained substrate.

The nocturnal feeding behavior observed showed 1/10th of the colony at the surface eating in the vicinity of their burrows. No feeding aggregations are observed in this case, during the mating season. This behavioral difference during the night can be explained as a consequence of the nocturnal temperature which permits the sand to remain wet longer.

Comparison of Uca crenulata Feeding Behavior and Feeding Mechanism With Other Uca Species

The Uca crenulata feeding activity remains around the burrow entrance or in feeding aggregations. This observation differs from Christy's (1980) observation of Uca pugilator; this specie does not feed around its burrows, and during feeding time they leave their burrows (breeding or temporary) located in the extreme upper intertidal or supratidal zone and move down the beach to the water's edge or poorly drained substrate. Christy uses Miller's (1961) observations of feeding behavior to explain U. pugilator's choice of substrate. When fiddler crabs feed they flood their mouth-parts with water withdrawn from the gill cavities. Due to evaporation from the buccal cavity while feeding, the crabs must periodically replace lost water by taking up soil moisture through seatal tufts located between the third and fourth walking legs (Miller, 1961). In areas where U. pugilator burrows, the substrate may not contain enough moisture to permit the crabs to replace water lost when feeding. This could explain the feeding aggregation formations along the water's edge.

The fact that feeding around the burrow entrance is absent in Uca pugilator is perhaps due to differences in burrow location and amount of substrate drainage.

Uca crenulata, as shown in this study by the soil texture analysis, feeds on sandy substrate. The Bouyoucous method (1928) used in this study to analyze soil texture, is similar to the one used by Miller (1961) in his observations of the feeding mechanisms in fiddler crabs. The observations made in the field and laboratory, as related to the *U. crenulata* feeding mechanism, are not comparable with Miller's more detailed observations (1961) on *U. pugilator, pugnax* and *minax*, but do allow us to make suppositions about the following:

A similar feeding ground, consistency and size of feeding balls, as well as water need between *U. pugilator* and *U. crenulata* could lead to similar feeding mechanisms. This supposition takes on more significance when you consider the close relationship between the substrate fed on and the anatomy of the mouth parts discussed by Miller (1961).

MATING BEHAVIOR

Color Variations

Crane (1944) observes four types of normal color changes in Uca: diurnal darkening, submergence darkening, darkening on capture and display brightening.

The variation of color from dark brown to white associated with the breeding season and the development of the display color is observed in many species of Uca. The display brightening includes chelipeds and ambulatory legs as well as the body carapace. A trend throughout the genus is toward the development of complete whiteness in both sexes during the display season (Crane, 1944). In the case of Uca crenulata, the development of a display color is observed only in the mating portion of the male population and is practically nonexistent in females (1/100). During the non-breeding portion of the year, both males and females display dark coloration. The carapace is brownish gray while the major chela of the male varies from a cream beige to light gray. As the mating season approaches, the mating male crabs undergo behavioral changes associated with their color changes.

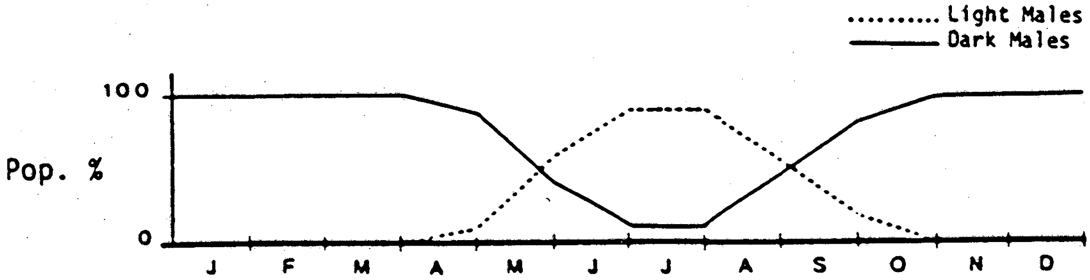
--The non-mating male population retains the dark carapace. Colors develop only on the major chela and inner side of the walking legs. The major chela coloration varies from yellow to orange while bright red can be observed on the inner surface of the walking legs and on the inner side of the merus.

--The active mating male population develops a bright display coloration. This change includes a carapace that varies from cream to white, walking legs with pink inner surface, white to pink small chela while the major chelipeds display a white outer surface and a white to pink inner surface. The two types of males present during the mating season will be referred to as light and dark males depending upon their carapace color. It is well understood that the dark summer male differs from the dark winter male by bright coloration on the major chela as well as on the inner side of the walking legs. The color change begins in April so that by the peak of the mating season, two months later, less than 10% of the males located on the mating colony remain in the dark phase. As the mating ends, the display color disappears and the entire population turns dark again until the next breeding season (Fig. 16). The population index formula (Table 2) shows results comparable to those in Fig. 16.

Behavioral changes precede the color changes; mating males begin waving before their color change has been completed.

The opposite process occurs in the fall. By the end of September most of the crabs are dark, but some waving is

Figure 16. Variation of dark and light crabs with burrows in colony I. The count was made for each month of 1982 and shows the development of display color as well as its disappearance.


Light Males
Dark Males
100
0
Pop. %
J
F
M
A
M
J
J
A
S
O
N
D

is still observed. In summary, the period of color change is shorter than the behavioral change, but both changes are related to each other as well as the environmental factors of temperature and light.

Behavioral Variations of Males During Courting Season

During the winter, all crabs have a permanent burrow where they spend the high tide and intermittent hibernation periods. The highest density of burrows is located in those areas covered by the summer mating colonies, i.e. in Colony II (1981) and Colony I and III in 1981 and 1982 (Figs. 8 and 9). The crabs' daily activities, mainly feeding during the winter, are centered around the burrow. A change in general behavior patterns and burrow location is associated with the development of the breeding color changes.

Dark Males

Location on the beach. The burrows of the dark males are located outside the mating colonies and have an average depth of 10 cm. Any attempt by the dark males to establish a burrow in the area inhabited by courting males results in aggressive interactions between the dark foreign males and the light resident males. The percentage of dark male burrows located in the breeding colony never exceed 10% of the total number of burrows in the colony.

Daily routine. As mating season approaches, dark phase males randomly choose a burrow at each high tide and occupy it during that tide (temporary burrow). As soon as the tide ebbs, these crabs leave the burrow and form dense feeding aggregations with other dark males and females and feed at the receding waterline. Four hours after the beginning of ebb tide the feeding aggregations break up and groups of animals start moving up the beach toward the permanent courting colonies; however, a significant portion of the population remains on the water's edge and moves up only as the rising tide pushes them up the beach. This movement of individuals, especially the females, stimulates the waving behavior of the light colored male crabs which have remained near the mouth of their burrow sites.

Light Males

Location on the beach. The light males' burrows are located in specific areas on the beach and remain at the same location for the entire length of the breeding season. Many are observed in the same location within the colony for the two consecutive years of observation (Col. 1, See Figs. 8 and 9). The burrow structure is composed of a main channel that can be as deep as 45 cm. Branches from the main tunnel lead to breeding chambers where the female incubates her eggs.

Daily routine. The light male stays at the breeding burrow's entrance during each low tide. Most individuals stay with the same burrow for the entire season if possible. The males defend their burrows against other males and concentrate their behavioral activities within a range of 5 cm around the burrow entrance except for frequent trips down the burrow to moisten their gills or for enlargement of the burrow.

Courtship Behavior

Male's Waving Display in Uca Species

The social behavior of fiddler crabs (genus *Uca*) is mediated by a variety of visual, tactile and acoustic displays. These movements are particularly striking in males because they possess an enlarged claw which is the principal effector organ for most of the signals (Salmon, 1967). During courtship, males attract females by a repetitive species-typical movement of elevation and lowering of this appendage known as waving (Crane, 1957). In her publication concerning the basic pattern of display in fiddler crabs, Crane (1957) describes in detail the two main types of waving patterns characteristic of the fiddler crabs. The waving behavior is observed during the breeding season and is associated with some species-specific motions which include elevation of the body by extension of the ambulatories. This motion is accomplished by rapid lowering and raising of the body on one or both sides, which results in the elevation of the entire body or the side containing the major chela. This behavior makes the animal more conspicuous. Most of the species of Uca may be clearly divided into two groups, depending on the type of wave pattern that is used. These two groups have been termed the "narrow-fronts" and "broad-fronts." The vertical wave display, characteristic of the "narrow-fronts," is a movement of the major chela restricted in front of the eyeballs, in which the cheliped is never flexed (Crane, 1957). The lateral wave, characteristic of the "broad-fronts," commences with a sweep to the side and is later followed by an elevation of the chelae which is finally flexed once more in front of the buccal region (Crane, 1957).

A difference in behavior is associated with the two following wave patterns:

Display in "narrow-fronts": During the final stage of pre-mating behavior, the "narrow-fronts" male pursues the female or approaches her at the mouth of her burrow. There is no marked increase in tempo of waving during the approach and when within reach, the male seizes the female and attempts copulation at or near the mouth of her burrow.

Display in "broad-fronts": The male precedes the female down his own burrow after a high intensity waving display. There is an increased tempo of display at the approach of the female and the female may or may not follow the male into the burrow. The female may stay below, or she may emerge shortly and continue her feeding.

Waving and Courting Behavior in *Uca crenulata*

Dark males. *Courting behavior*. The dark male does not have a burrow into which he can attract the females and thus he is limited to the pursuit of females on the beach surface. This approach is not very successful and is not common in *Uca crenulata*; however, this behavior has been described by Crane (1957) as typical behavior for "narrow-fronts" species and has been observed occasionally in *Uca crenulata* colonies.

Waving display. The dark males do not wave while in feeding areas or outside the "white" conoly, however they do occasionally display waving behavior as they cross into the courting colony and are in close proximity to the waving white males. The number of dark males that succeed in mating is small (3 males in 72 days of observation). The dark male waving pattern is similar to the "broad-fronts" *Uca* described in the introduction but the rarity of their waving display made film documentation difficult. Field observations provided the data required. Because of the waving pattern and courtship behavior, I would suggest that we consider the dark crabs as an intermediate between "broad-fronts" and "narrow-fronts."

Light males. *Courting behavior*. The main activity of light males during low tide periods is courtship behavior. This activity consists mainly of waving at passing females and defending the home territory. Waving display was observed for periods ranging from 2 to 4 hours (1/3 to 2/3 of intertidal periods). The loss of a crab's breeding burrow as a consequence of a fight causes him to cease his courtship behavior. Light males which have been evicted from their burrow and are unable to find a substitute burrow within a short period of time (.5 hr.) will usually wander down to the water's edge and join the feeding aggregations formed by non-displaying males. The extremely low number of light crabs observed in feeding aggregations suggests that evicted males either find a burrow before the next low tide or lose their display color as a consequence of their breeding burrow loss. The inability to mark these animals made verification of these ideas impossible. The light male has the typical courtship behavior of the "broad-fronts" Uca and following a high frequency waving display, precedes the female down his own burrow. The female may follow the male down the burrow but may not stay below where copulation presumably takes place (Crane, 1957). Their main activity is to wave at females in an attempt to induce them into their burrows. For this reason, all other activities become secondary and are interrupted if a female comes by. His daily activities of building and defending a burrow are geared to give him the maximum chance of being successful in courtship.

The waving behavior of the male seems to be stimulated by two main factors:

(i) Movement of individuals within the colony,

(ii) Noise and movement produced by other waving males.

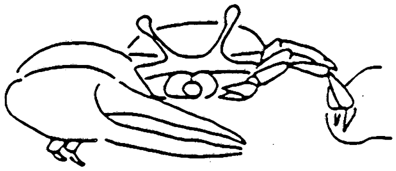
(i) The movement of a female through the colony triggers the waving behavior. The males' visual ability does not seem to be sharp; consequently, some dark males, prospecting for new burrows, approach the waving male by mimicking a female (by keeping their major chela close to their body). In this manner dark males may enter the burrow of a mating male without fighting. At the beginning of the mating season, certain females with red legs appear to induce more waving than the others.

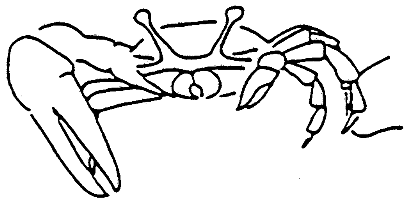
(ii) If a female enters the colony while most males are in their burrows, the waving of one or two males which are still at the surface is sufficient to attract all other males from inside their burrows. They rush out of the burrow waving excitedly with no particular direction to their display behavior. It is only when the female is very close that they will adjust their waving to focus on the approaching female. The female's response to the male's waving varies and will be discussed more in detail later. If the female follows the male into the burrow and remains in the burrow, occasionally neighbor males try to enter the burrow in an attempt to attract the female.

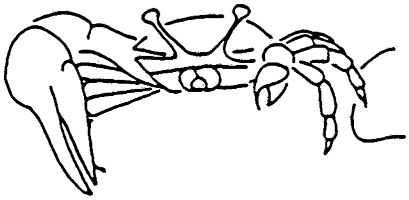
If the burrow owner repels the intruder, he will alternate between the burrow and the entrance for a few seconds. Then he remains in the burrow with the female for a time, eventually returning to the entrance to guard the burrow and wave at other females.

Waving display. The sequence of the waving display shows a typical lateral extension, vertical lifting and then lowering of the major chela. This sequence is the characteristic waving pattern of the "broad-fronts" species of Uca (Crane, 1957). The rate of movement of the major chela varies with the proximity of a female. If no female is present, the waving display is of low frequency with a reduced lateral extension and vertical elevation (Fig. 17). This low frequency waving appears to be initiated spontaneously and is usually observed during the first few hours following the beginning of ebb tide. This slow wave frequency repeats itself with a cycle of 4 to 6.5 seconds. Once the routine behaviors of feeding and burrow building are completed, this spontaneous waving appears in 40% of the light males provided the ambient temperature is 20°C or above. This behavior is more common during June, July and August which are the months that comprise the bulk of the breeding season. Prior to the main breeding season (April and May) the presence of a female is necessary to induce any type of waving behavior. In low frequency waving the minor cheliped rarely accompanies the movement of the large chela and no lifting of the ambulatory legs is observed. The high intensity waving display observed (Fig. 18) during active

Figure 17. Wave pattern of *Uca crenulata* is absence of a female: slow movement (4-6.5 seconds) with a reduced lateral extension as well as vertical elevation.







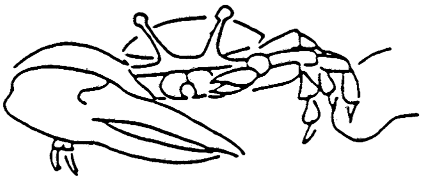
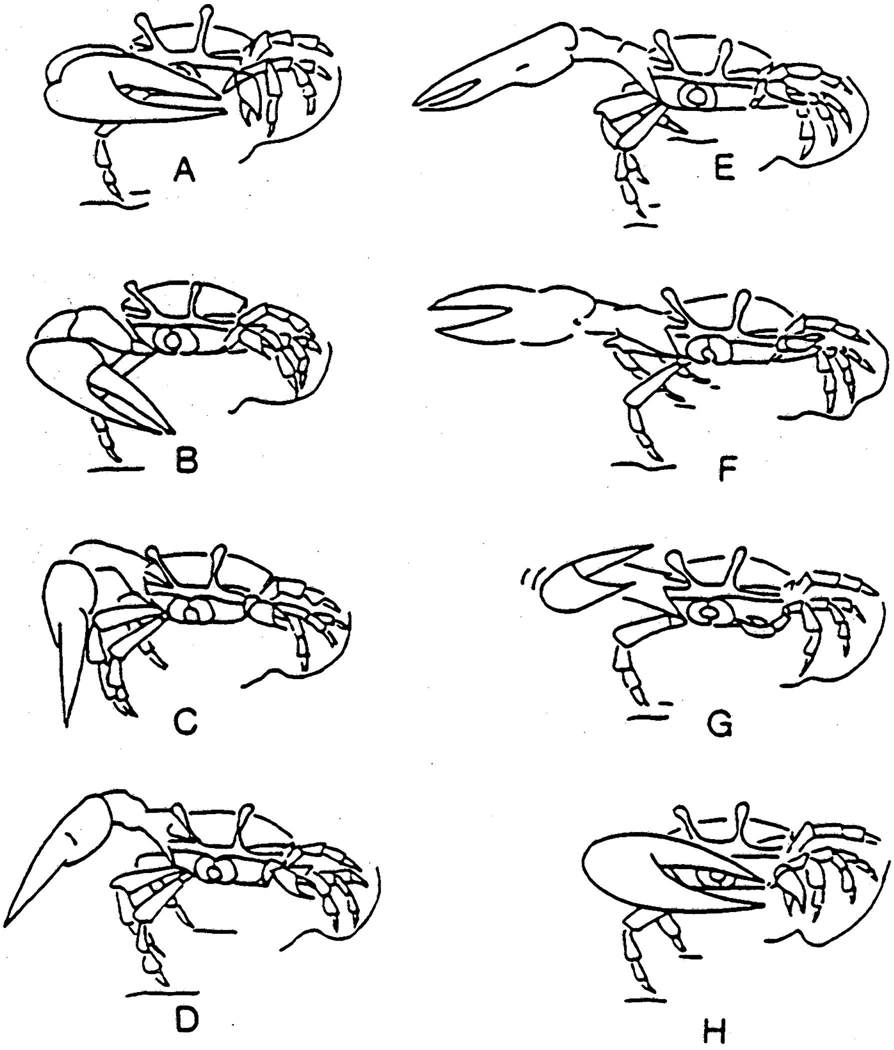


Figure 18. Wave pattern of *Uca crenulata*, (female in proximity).

A-B-C	lateral extension
D-E-F	vertical elevation
G-H	lowering of claw from the maximum extension angle to the beginning point.


A
B
C
D
E
F
G
H

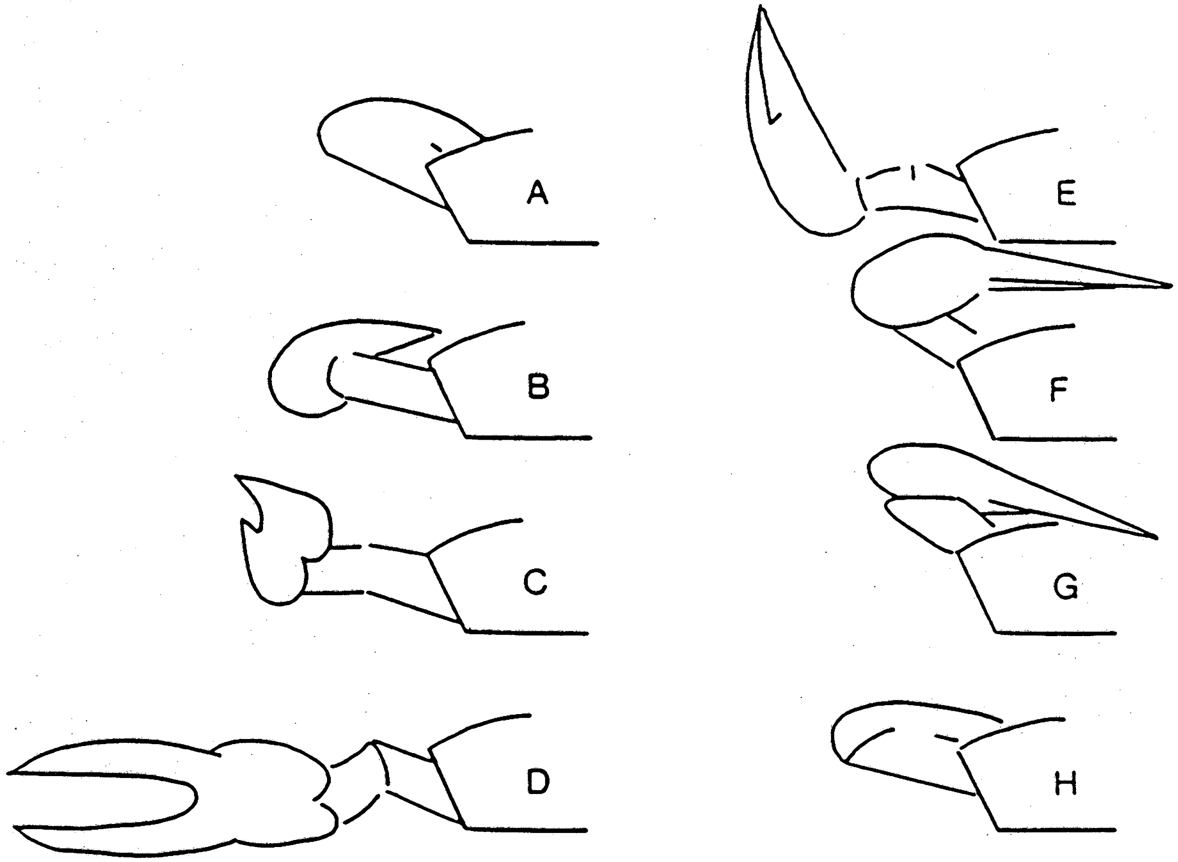
mating periods is evoked by the approach of other crabs, usually females.

Dark males may also induce waving. When the burrow owner realizes that he is not waving at a female, but at an adversary intending to steal his burrow, he switches from display to antagonistic behavior or avoids combat by going down his burrow, using his large claw to block the burrow entrance.

When a female approaches, the male increases the waving frequency and lifts the walking legs on the side contralateral to the waving chela. He also moves a few cm away from his burrow entrance toward the female as if to gain her attention. This high frequency wave repeats itself with a cycle of 1 to 5 seconds: Smaller crabs display slower waves than adults and the early months of the breeding season as well as the early hours of the days are characterized by a slower waving movement. The speed of the wave increases in June, July and August, as well as in warm afternoons of the breeding season. A typical high intensity waving display begins with a lateral extension of the chela to the side. The chela is then lifted vertically to an angle of 15 degrees, as compared to the beginning location in front of the eye stalk. During this vertical lifting the claw is also extended behind the front edge of the carapace (Fig. 19). The two first sequences forming the wave movement, lateral extension and vertical elevation are very slow

Figure 19. Rear view of the wave pattern, (female in proximity).

A-B-C-D	lateral extension and vertical elevation (0.5 to 4.5 seconds).
E-F-G-H	lowering of the claw to the original beginning point (0.5 seconds).
D	the large claw is extended behind the carapace


A
B
C
D
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H

compared to the rapid lowering of the claw toward the original position in front of the eye stalk. This final sequence, going from the maximum point of lateral extension to the beginning position has been observed in 20 crabs and takes an average of 11.5 images (movie speed 24 images/sec.) which corresponds to 0.5 seconds.

Size Relationship of Mating Males and Females

This problem has been approached in 1980 by Christy during his observations of *Uca pugilator*. He studied the male and female relationship by examining the size of 85 pairs that had enclosed themselves in a breeding burrow. This method cannot be used with *Uca crenulata* due to the extremely low number of females which remain in the male's breeding burrow. In 72 days of observation only 4 were observed to remain within the burrow. An alternate method was to make precise counts of the mating males found on the colony surface as well as the gravid females found in breeding chambers. The animals were divided into 3 categories based on size:

(1) large, carapace width over one cm
(2) medium, carapace width of 0.5-1 cm
(3) small, carapace width less than 0.5 cm.

The small and medium adult males and females are able to court; however, adult males (over 1 cm in width) constitute the distinct majority (73%) in courting. Only

10% of those courting were in the small category (Fig. 20). The mating female population showed less size variation. Fewer adults and more medium and small females were found to be gravid (Fig. 21). Different suppositions can be made to explain this variation between mating males and females. The mating colony was located at a higher elevation and, as we saw earlier, adult mating males have a distinct preference for upper beach location (tide level +4.4 feet). For this reason, most of the individuals inhabiting colony I will be adult (over 70% in this case) and the small crabs must compete with individuals 2 to 3 times bigger than themselves to maintain a breeding burrow in the colony. This strong competition may explain the paucity of small crabs present in the mating colony, about 10%.

The female's situation is quite different. The burrow entrance is an important factor in the female choice. The entrance is determined by the carapace length of the occupant as crabs enter their burrow "sideways." Thus, females can mate only with males their size or larger (Christy, 1980). This observation made on <u>Uca pugilator</u> also applies to <u>Uca crenulata</u>. Field observations show that adult females are unable to enter burrows with an entrance that is too narrow while medium and small females could respond to the waving of most of all sized crabs. The results gathered in Figs. 20 and 21 confirm these field observations and show that larger numbers of medium and small

Figure 20. Percentage of the courting male population durin
July and August 1982 and size variation. N = sample number.

Size of Courting Males in Colony I

Average % for July: l: 81%
m: 18%
s: 1%

August: l: 62%
m: 28%
s: 10%

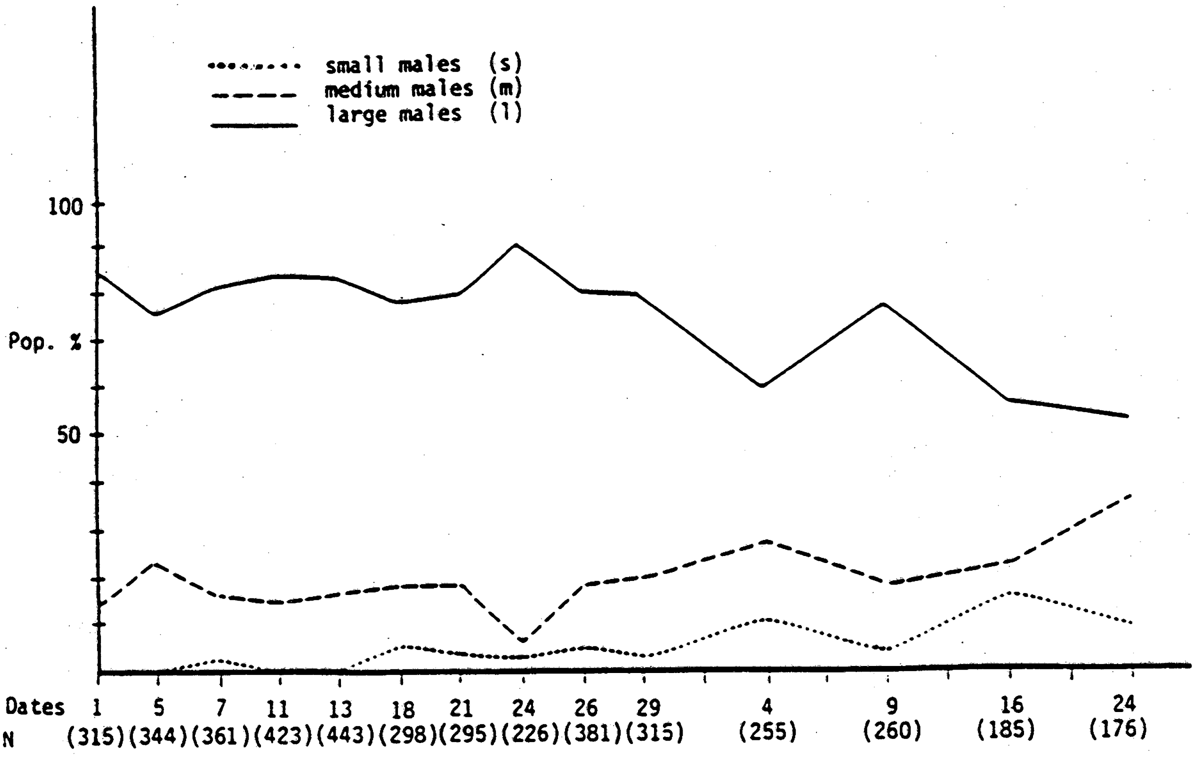
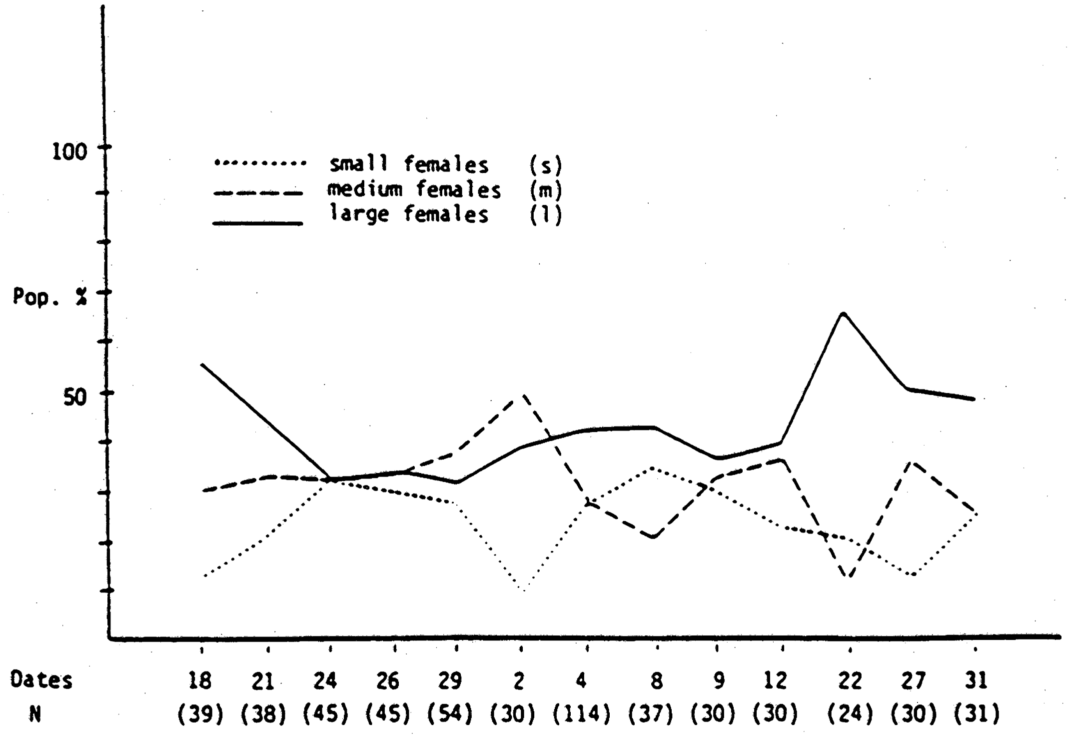


Figure 21. Percentage of the breeding female population during July and August and variation of their respective sizes. N = sample number.

Size of Breeding Females

Average % for July: l: 40%
m: 35%
s: 25%

August: l: 45%
m: 35%
s: 20%



females can successfully mate as compared to males of the same size. Christy (1980) did not observe any tendency for females to mate preferentially with males their own size and mentions the case of small females mating with adult males in the case of *Uca pugilator*. The results obtained for *Uca crenulata* show clearly the existence of mating taking place between large males and small females, a fact which is not mentioned in the study of *Uca rapax* made by Greenspan in 1975.

Mating Behavior and Reproductive Cycle

Female's Mating Behavior

A female can respond in various ways to the male's courtship behavior:

(a) ignore the male,

(b) check the burrow, by inserting her walking legs into the entrance,

(c) enter the burrow after the male then exit after a few seconds' examination,

(d) follow the male into the burrow and remain inside.

We assume that mating occurs if the female stays in the burrow. The behavior of non-gravid females differs considerably from the behavior of the gravid females. During the low tide feeding period non-gravid females are not observed in the mating colony, as they are foraging for food at the water's edge as part of the feeding aggregations. As the tide comes up, they are pushed by the water and begin searching for temporary burrows, either outside the male's colony or in the mating male colony. The females which leave the feeding aggregation last appear to be more receptive to male courtship. The burrow structure appears to have a more important role than the male himself in the female's choice for a burrow site. The gravid females found at the surface of the sand do not mix with the feeding aggregations. If gravid females are found on the water's edge, they represent a very low percentage (0.5-3.0%). They spend the low tide period feeding around or in the male colony; and as the tide returns, they only look for burrows in the male colony. Usually, they enter an empty burrow; however, occasionally they respond to a male's waving and will follow him down into his burrow. The G females represent 1/10 to 1/5 of the females found on the male's colony during the mating season. The G females present at the sand's surface are only a small proportion of the total number of G females actually present in the colony, since most of the G females remain in the breeding chambers from the time they mate until the eggs are released.

Reproductive Cycle

The reproductive cycle and breeding season of *Uca pugilator* was studied by observing the females entering males' burrows in response to the males' courtship behavior (Christy, 1980). The same method was used during two summers that species Uca crenulata was studied, without success. Only 4 females were observed to stay in males' burrows during the two seasons of observations. For this reason, it was decided to approach the problem from a different perspective and to observe gravid females. Gravid females found in designated burrow sites, ranging from 1 cm to 45 cm in depth, were brought to the laboratory where eggs were observed and categorized as to the stage of development. The stages of development from deposition to the larva stage were divided into identifiable stages.

In the laboratory, it was impossible to study the development of eggs from Stage 1 to 8 on any one female. In nature, gravid females usually stay in the breeding chamber until it is time to release the larva. The trauma of digging out and then burying of the animal decreased the female's ability to retain her egg cluster as long as it is carried in nature. Variation in environmental conditions and stress also contributed to shorter carrying times in the laboratory.

To compensate for this difficulty and to evaluate the length of the gravid period I used a combination of two methods:

(a) Staging and synchronous incubation of separate egg clusters,

(b) Staging of egg samples taken from ± 30 field animals every 3 days over a 6-week period.

(a) Determining development stages of large groups (30 animals) of egg clusters in the lab allowed a detailed description to be made for each distinct stage. Two distinct markers could be used in determining the stage of development. First, the percent of yolk present was a consistent marker and clearly identifiable. Second, appearance of embryonic structures provided distinct markers for staging embryonic development. The stages identified (Fig. 22) were:

Stage 1. Complete yolk dispersion

Stage 2. Appearance of a clear vitelene space

Stage 3. Yolk and pigment comprising 2/3 of egg

Stage 4. Yolk comprising 1/2 of egg and first appearance of eye pigmentation

Stage 5. One-third yolk and appearance of notochord pigment

Stage 6. Eye pigment forms a complete sphere

Stage 7. Beginning of eye cup structure

Stage 8. Eye cup complete

Stage 9. Larva complete

The observation of the egg stages for a few consecutive days after they were brought into the laboratory and initially identified, was done for all G females which were captured every three days from the study site. Figure 23 illustrates

Figure 22. Embryonic stages of *Uca crenulata*. —0.1 mm

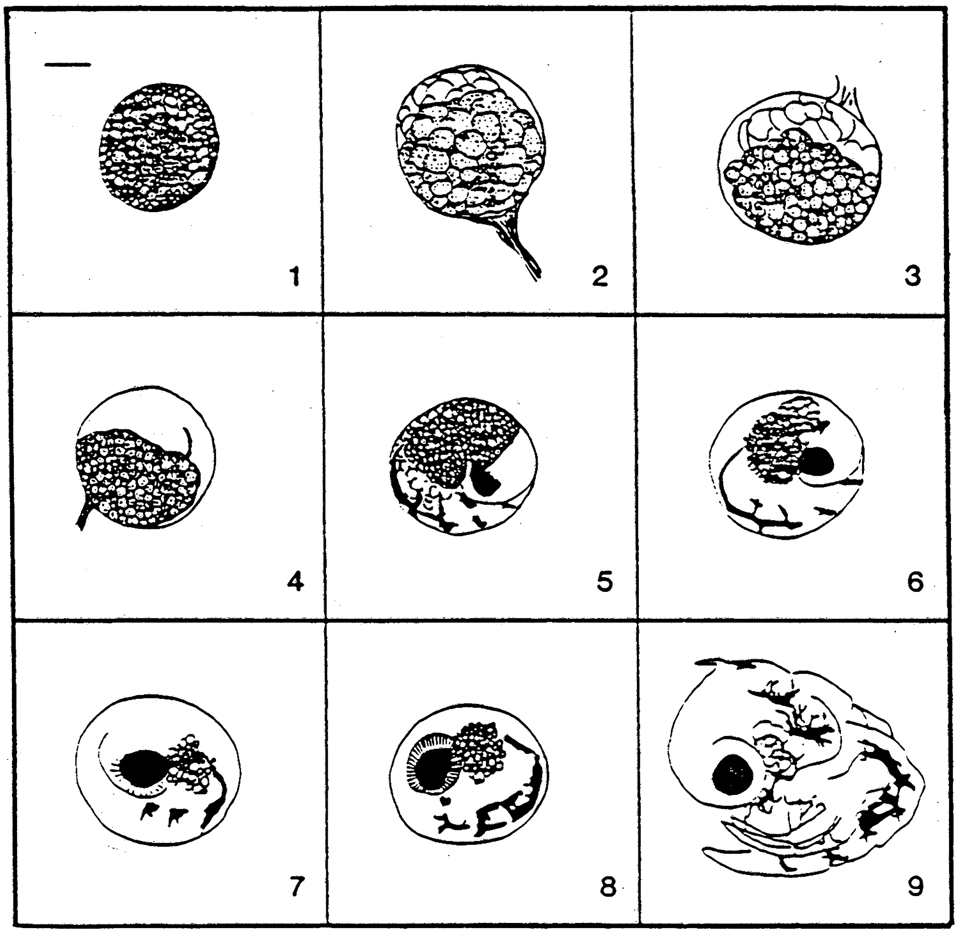
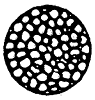
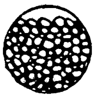
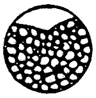
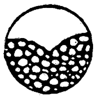
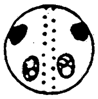

1
2
3
4
5
6
7
8
9

Figure 23. Results of incubation and staging of eggs.

Egg Stages	24 July	27 July	30 July	1 August	
	1	1			Number of females carrying eggs at each specific stage.
	3		1		
	6	5		1	
	8	3	6	2	
	11	7	1		
	4	8	2	5	
	3	11	7	2	
		1	10	1	
Female With No More eggs.			9	25	

this method. In this special case, it takes 6 days for the majority of eggs (Stage 5) to reach the final stage of the larva release (Stage 8). The combined study of many of these tables showed that the majority of animals reaches Stage 5 at day 6 and the larvae are released on day 12. In some cases, 15 days were required for incubation. When the exact mating time was observed and the female was brought to the laboratory, it was noted that egg deposition was complete in 3 days. Thus a normal breeding cycle from fertilization to deposition of the eggs is normally 15 days in _U_. _crenulata_.

(b) Once the incubation time had been determined, the second method was employed to determine to what extent the entire population was synchronized in its breeding pattern. Approximately every 3 days, thirty or more gravid females were collected and returned to the lab. Egg samples were taken from each female and the stage of development was determined. This procedure was continued from July 18 through August 30 of 1982. The data of these observations are shown in Figure 24.

The stage represented by the majority of females is considered as being dominant and representative of a specific time in the reproductive cycle of the femal population. Egg's Stages 1 and 2 illustrate the beginning of this period while Stages 7 and 8 end it. Figure 24 represents the egg stages found in gravid females in July and August

Figure 24. Egg stages of female populations taken from study site during July and August 1982.

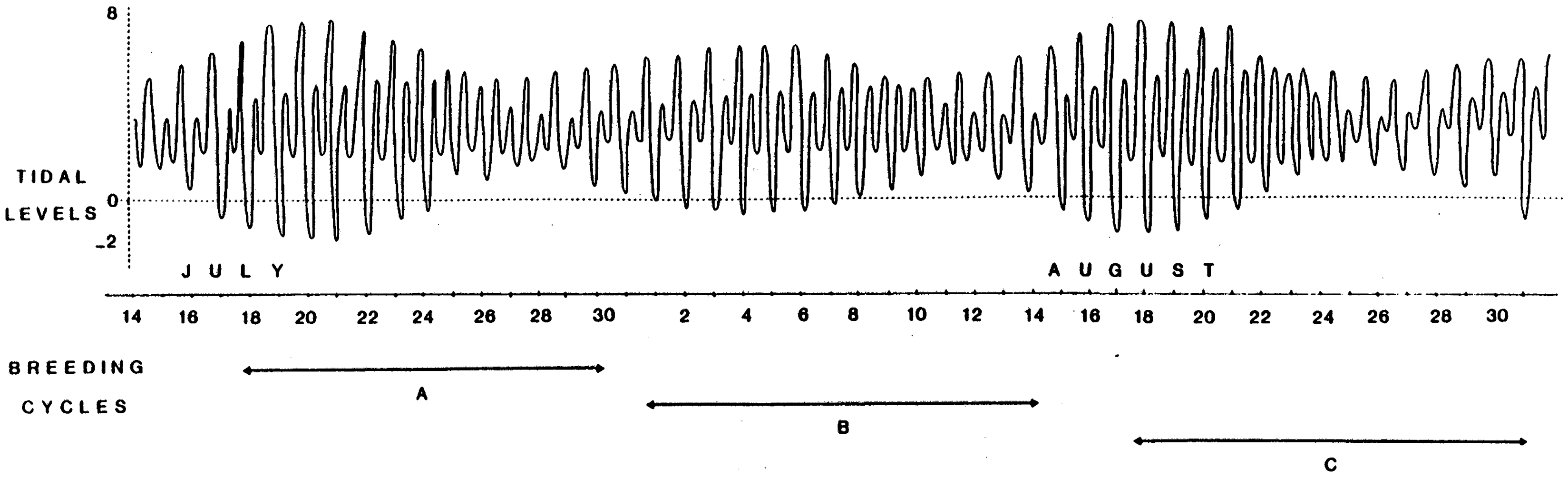
EGGS STAGES	DATES OF CAPTURE OF GRAVID FEMALES														
	JULY					AUGUST									
	18	21	24	26	29	1	4	7	9	12	17	19	22	27	31
	⑭	5	1	1	5	⑦	6	1	1	8	⑨	0	0	0	0
	7	5	3	6	⑧	2	⑧	3	1	1	2	8	5	0	0
	3	⑧	5	6	6	3	4	3	2	1	3	0	⑪	1	0
	2	6	6	4	3	3	3	⑪	4	1	0	4	4	2	1
	2	1	⑨	3	4	6	2	5	6	2	1	4	3	5	2
	1	2	3	⑧	3	2	2	1	⑦	6	1	0	1	⑨	7
	1	2	3	2	1	3	3	3	6	⑪	8	0	5	8	9
	0	1	0	0	0	4	2	3	3	0	6	⑭	1	5	⑪

1982, and the best represented stage (circled number) varies with the time in the month. For instance, on the 15th day of capture (August 1), half of the female population carried eggs in Stage 1, 3 days later the majority of eggs were in Stage 2, on the 21st day (August 7) they were in Stage 4, on the 23rd day at Stage 6 and on the 26th day they were at the final stage. The same progression in egg stages was seen in July and the end of August. Studies made on U. pugilator, U. rapax, U. pugnax and U. minax (Greenspan, 1975); Christy, 1980) showed that the time for mating to larval release was about 15 days.

Once the breeding cycle was established, the influence of environmental factors, mainly the tidal pattern, could be observed. Figure 25 compared the results of Fig. 24 with the tidal pattern of July and August 1982 and indicated that 3 breeding cycles could be observed between the 18th of July 1982 and the 31st of August 1982. Many authors (Christy, 1980; Greenspan, 1975; Zucker, 1978) observed a relationship between the tidal pattern and the release of the larva. U. pugilator females released their eggs predominantly on the neap tides (Christy, 1980). U. musica, U. beebei and U. latimus released their larva on the highest amplitude spring tide each month regardless of whether these tides occurred after the new or the full moon (Zucker, 1978). Uca crenulata females appeared to release their eggs during

Figure 25. Relation between tidal pattern and breeding cycle during the mating season (1982) A, B, and C represent the 3 breeding cycles observed during the 6 last weeks of the mating season.

RELATION BETWEEN TIDAL PATTERN AND BREEDING CYCLES



spring tides. The *Uca crenulata* mating habits and breeding cycle were difficult to determine because the exact mating behavior and time were not observable. The study of gravid females during 6 weeks of the breeding season suggested 3 breeding cycles of approximately 15 days duration which ended during the spring tide. Presuming that the breeding cycle lasted 2 weeks, this suggested that mating occurred during the previous spring tide. More observations would be necessary to give precise results.

The females observed before July 18 were not numerous enough to use the data but they gave a time base for suggesting that in the Carlsbad population of *Uca* there were three main breeding cycles with a minor cycle early in the season and a minor one again at the end of the season.

Five hundred G females of different sizes and ages have been observed in 6 weeks and while the majority were adults, 1/7th of them were born the previous year. The proportion of males, G females and NG females found in specific square meters was determined. The number of G females during the peak breeding season (August 4) and during the declining of the breeding (August 31) was determined.

August 4		August 31	
45 males		25 males	
16 NG females	m2	15 NG females	m2
18 G females		5 G females	

Fifty-three percent of the females were gravid August 4 and 21% were gravid August 31.

Crane (1975) has suggested that in species of *Uca* where males court from burrows, the aggregation of waving males resembles leks. Leks are aggregations of courting males, usually at traditional locations, to which females come solely for the purpose of mating.

U. *crenulata* G as well as NG females are found in the male's colony, so this colony cannot be considered a real lek where females go only to mate. Although the number of mating females was higher than the other females during the breeding season, a large number of females used this colony for food and burrow resources, making the male's colony only a lek-like organization.

DISCUSSION

Color Changes Associated With the Breeding Season

Possible Hormonal Control

The color variation associated with the breeding season of *Uca* species has been studied in detail by Crane (1941, 1944). However, my observations of the *U. crenulata* population in the "Aqua Hedionda" lagoon, differs in some aspects. The daily transition from dark to yellow, and then to the final white stage is not observable in *U. crenulata*. Mating males appear to maintain the light stage during the entire breeding season and do not lose their light coloration after capture, as is the case with *U. latimus* and *stylifera*. The color transitions described by Crane, can nevertheless be observed preceding the breeding season. Dark male *U. crenulata* that maintain a burrow in the mating colony will progressively lighten. They will progress through a yellow stage and then finally reach the white stage. As mentioned in the results, the behavioral changes associated with the breeding season precede the light color stage, appearing during the transitional phase of the color change.

Since maximum lightening occurs in the display season and is intimately connected with a courtship behavior and is almost non-existent in the dark population, it seems likely that factors responsible for the color change are the same as those that initiate the behavioral changes. The most likely candidates for this major change are the sex hormones.

Thermoregulatory Advantage

The light phase appears to have a valuable thermoregulatory function in the case of U. crenulata, at least for the males which remain on the surface near the entrance of their burrow during the duration of the breeding season. This type of behavior differs from those species which display at the entrance of the burrow for only a short period of time and then wander with the feeding associations at the water's edge (U. pugilator). The U. crenulata male spends many hours at high temperature on the sandy beaches, and his light carapace decreases its absorbing ability and increases reflectance. The thermoregulatory advantages of a light carapace during the breeding season can be compared to the blanching process observed by Wilkens and Fingerman (1965) in a normal population of U. pugilator. This change was independent of the breeding cycle and was exclusively in response to high temperature.

When the seasonal temperature changes (Fig. 5) are compared with color changes (Fig. 16) and behavioral activities (Fig. 12), it can be seen that the male colony of Uca crenulata responds in two ways to the increased summer temperature. During mating season the lightening of the carapace allows the crab to display on the sand for hours

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during the high ambient summer temperatures. As the mating season ends, the light carapace darkens again and the crab decreases its range of activities. This change in behavioral activities decreases the time spent on the surface and protects the population from the high temperatures which can occur in September, October and November. In conclusion, a color change is associated with the breeding season and has thermoregulatory advantage to the crab. This color change is not just a result of an environmental temperature increase because the crab has other ways to adapt to high temperatures as is previously described (p. 28). The color change associated with the breeding season may be caused by endogenous variations, possibly changes in the level of sex hormone. Temperature may influence hormone release; consequently, it is only indirectly related to the lightening process characteristic of the mating season.

Relation Between Waving Frequency and Visual Field Stimulus

Comparison Between U. crenulata and Other Uca Species Waving Display

The waving sequence and its frequency has been studied in many *Uca* species and some variation in sequence and speed has been observed. *U. minax* and *U. pugnax* complete one single wave in 2.50 seconds while *U. pugilator* takes 1.25 seconds. The degree of extension of the major cheliped varies also. The time required to bring the major cheliped from its extreme point of extension to the original location varies from 1.25 seconds in U. minax and pugnax to .50-.70 seconds for U. pugilator. The waving pattern of the U. crenulata males is studied in the field and is similar to U. pugnax (illustrated by Salmon, 1968). The total time to complete the wave varies from 1 to 5 seconds, but the time necessary to bring the major cheliped from its extreme point of extension back to the original location is .50 seconds (cf. U. pugilator). These results show that there are noticeable differences in the waving display of different species and these differences may be important for inter-species discrimination especially if the visual system of the crab is able to discriminate between the different patterns of waving.

Visual Field as a Sensory Filter

Neurophysiological experiments show the existence of a special visual neuron in male and female U. crenulata (Rafuse and Hall, in preparation). The U. crenulata wave is formed by 3 different movements: lateral extension, vertical elevation and vertical downward movement. The female located at 5-15 cm from the waving male perceives the last part of the waving sequence as a vertical down movement of 30-40° per second. The optimum stimulus of the neuron studied in U. crenulata is a vertical downward movement of 30 ± 3 degrees per second. The frequency rate (30-40°/second) of the ce of male *U. crenulata* is in the range seen by wavin . Thus a sensory neuron in the eye of the female o act as a rate sensitive filter in selecting males own specie. The modality specificity of this visual on is thus an excellent example of an afferent neuron acting as a species-specific filter in mating selection and could be of value in areas where *Uca* species dwell sympatrically.

U. crenulata males do not distinguish between females and those males lacking a major cheliped. The male courtship behavior is displayed toward both groups. No experiments have been done to show if *U. crenulata* is species-specific in its waving behavior.

The demonstration of a sensory neuron acting as a rate sensitive filter in the female's eye suggests that in *U. crenulata*, as in *U. pugilator* (Aspey, 1971), the female selects the mate while in *U. pugnax*, the male makes the selection. More research showing the existence of a visual field in *U. pugilator*, similar to the one of *U. crenulata* as well as its absence in *U. pugnax*, could explain the behavioral differences observed by Aspey (1971) between the different *Uca* species.

Crane (1941, 1957) and Salmon (1965) reviewed the early studies on fiddler crabs, especially those related to waving. They established that the waving was characteristic of virtually every species, differing only in sequence and rate. If the particular visual neuron found in the *U. crenulata* female exists in other species, and if the frequency rate of the male's wave for each species corresponds to the optimum stimulus of the conspecific female visual neuron, one could have a physiological base for the various waving behaviors among *Uca* species.

Mating Behavior

The daily activity profile of the mating males showed in Fig. 13 illustrates an important waving activity characteristic of the breeding season; however, there are two observed exceptions, one on the 7th of July and the other on the 4th of August 1982. On both days there is an unusual paucity of waving behavior considering that the temperature is warm and a low tide occurred in the middle of the day.

Christy (1980) mentions that there are cycles of reproductive activities in male as well as in female *U. pugilator*. Female sexual receptivity peak coincides with the male reproductive activity peak which occurs about four to five days before each spring tide. He finds two groups of synchronized females. Females from each group mated a few days before alternate spring tides. These females also were closely synchronized in their release of larvae, which occurred predominantly during neap tides.

These observations of *U. pugilator* behavior may provide an explanation for the low waving activity present on July 7 and August 4 which in each case could correspond to the end of the male reproductive cycle. Figure 25 compares the tidal pattern with the females' breeding cycles, and illustrates the relationship between the low waving activity of the 4th of August and female breeding cycle which appears to be initiated at the beginning of August. Only three breeding cycles were observed during the last 6 weeks of the breeding season of 1982. The small number of gravid females brought to the laboratory for egg stage identification before July 18 are numerically insignificant, but they suggest that two breeding cycles could take place between June 15 and July 18. Under these conditions, the non-mating activity observed on the 7th of July coincides with the first 1/3 of a female breeding cycle occurring at the beginning of July.

The two breeding cycles observed in August may belong to two synchronized groups of females as described for U. pugilator (Christy, 1980). The beginning of the male reproductive cycle would correspond to the middle of the female breeding cycle. At that time, half of the female population is gravid and in breeding chambers while the other half is receptive to the male waving behavior. The male would display 10-12 days, mating with the receptive female population and would end his reproductive cycle at the time when half of the female population is depositing eggs, while the other half has just released their eggs and are not yet receptive to males.

Females do not appear to mate at a specific time of the month, but egg deposition is synchronized. This suggests that following mating, the sperm is stored until the time of egg release when the eggs are fertilized and thus development is synchronized.

Cycles in the Behavioral Pattern of Uca Crenulata

While observing the behavioral activities of the *U. crenulata* colony at Carlsbad certain repetitive patterns become obvious. The most apparent rhythm is related to the tides in the local lagoon, the second factor that influences the crabs behavior is temperature. The influence of these factors on the behavior of the crabs bears further discussion.

Tide Cycles

The lagoon in which the crabs are located is the second in a series of three, and as such the water entering the lagoon must pass through two successive inlets or narrow causeways. As a result, there is very little turbulence in the ebb and flow of the tides. The colony site is immersed and exposed twice every 24.7 hours. The height of the high and low tides determines the amount of time during which the animal is active on the surface, while the temperature determines how active the animals will be during that particular cycle. Therefore the tide regulates:

(1) the length of time spent above ground,

(2) the time of day spent actively,

(3) the type or sequence of activities performed,

Seasonal Cycle

The amplitude, timing and diversity of behavior varies with the season, warm days in the fall and winter are spent eating while a summer day of the same temperature is spent in burrow repair, defense and mating behavior. A low tide during the warm portion of the day, in winter or summer, dramatically increases the number of individuals on the surface.

Day Night Cycle

The behavioral activities during nocturnal low tides is very sparse or non-existent, showing a large difference between diurnal and nocturnal behavior.

In summary one can observe many cycles in the *U. crenulata* behavior. They depend on extrinsic environmental factors while the breeding cycle discussed earlier is influenced mainly by intrinsic factors.

Special Problems

The major problem faced in this study is the extreme rarity of the female response to the male waving behavior, however, one can be confident that mating does occur by observing the high density of gravid females found in the burrow chambers.

observations and information found in the litera- cerning similar problems could give a clue to this cular behavior.

It is not the first time that such observations were made by observers of *Uca* mating behavior. In 1947 Burkenroad studied *Uca pugilator*, and while he observed only one female following the male down into his burrow during the daytime, he reports many nocturnal pairings on the surface. Copulation occurred frequently on the feeding ground at night. Salmon (unpublished dissertation) also observed *Uca pugilator* copulating on the surface at night. Crane (1975) mentioned that in the eastern United States, nocturnal copulation on the surface appears to be common in *U. pugilator* and *U. pugnax* and also in the Spanish population of *U. tangeri*. However during the day, males from these species attract females underground, mating at the surface being rare. An exception is in Von Hagen's report (1962) describing in detail the surface coupling characteristic of *U. tangeri*. Most of the surface mating takes place around the female's burrow or at its entrance, and rarely are copulating pairs found at the water's edge (far from the burrows). The particular high percentage of nocturnal surface copulation is explained by the absence of nocturnal predators during the breeding season of 1960. In 1961 predators were as numerous at night as in daytime and consequently no surface copulation was observed. The diurnal waving behavior of *U. tangeri* is waving sequence of male *U. crenulata* is in the range seen by this neuron. Thus a sensory neuron in the eye of the female appears to act as a rate sensitive filter in selecting males of her own specie. The modality specificity of this visual neuron is thus an excellent example of an afferent neuron acting as a species-specific filter in mating selection and could be of value in areas where *Uca* species dwell sympatrically.

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These references to the existence of surface mating behavior and to nocturnal mating behavior in _Uca_ species displaying complex waving pattern, could explain the presence of a high density of gravid _U_. _crenulata_ females in spite of the absence of female response to male diurnal waving behavior.

The _U_. _crenulata_ population at Carlsbad is the subject of repeated night observations but poor visibility due to continuous nocturnal fog prevents precise observations. However, the crabs observed at night are very slow in performing feeding and fighting behavior, and their density on the surface is much lower than in daytime. No surface coupling is observed and may be explained by certain factors.

(a) Nocturnal mating seems to be restricted to a few specific nights of the breeding season. Von Hagen observed nocturnal coupling during only 8 nights in 1960. As Pearse (1912) mentioned full moon nights as being important in nocturnal mating, I made my observations on these nights but without any observable matings.

(b) The low temperature found at night in the lagoon may reduce the nocturnal activity of the crab. The _U_. _crenulata_ located along the Mexican coast are more active at night than the Carlsbad population (Dr. Rafuse's personal observations).

(c) The nocturnal observation is limited due to lack of proper illumination. As Crane (1975) mentions, the use of infrared illumination which is now available but not yet used by observers of *Uca*, would settle a number of questions concerning copulation at night.

Diurnal surface coupling is observed among *U. crenulata* wanderer male population. None of the actively waving light males are observed attempting surface copulation as is the case for *U. tangeri* (Von Hagen, 1962).

The presence of diurnal surface copulation as well as the possibility of nocturnal mating (Von Hagen and Burkenroad observations) suggests that *U. crenulata* of Carlsbad has a behavior different from the typical broad-fronts described by Crane (1957). But, among *Uca* species, mating variations seem typical and depend on locations and environmental factors. Christy (1980; and Christy and Salmon, 1984) considered the mating behavior of *U. pugilator* as a typical diurnal activity, while Burkenroad (1947) observed most of the mating at night. Von Hagen (1962) observed a large number of coupling at night during his first year of observation, but observed nothing during the next breeding season due to the presence of new nocturnal predators.

The supposition of the surface coupling as main reproductive behavior in *U. crenulata* does not bring in question the value of the waving display. This research shows the physiological value of this behavior and the absence of female response to it could be an adaptation of the female to special circumstances. The female _U_. _crenulata_ possesses a visual field which allows her to discriminate between different species of males and to have a conspecific mate in the case of species living sympatrically. But, in this case, the colony of _U_. _crenulata_ is isolated, and therefore the waving might lose some of its selective importance.

Another suggestion by Christy (1980) and Greenspan (1975) is that the females produce more than one clutch of fertile eggs after mating just once. This is accomplished by the female storing the sperm and releasing it only when egg deposition takes place. This procedure could explain why so many gravid females were observed and so few matings were seen in the population.

In summary, this research provides a detailed description of the ecology and behavior of _U_. _crenulata_ living in Carlsbad, California. _U_. _crenulata_ is the only fiddler crab living on the North American west coast. This study will be a reference point for comparing work on the fiddler crab of the east coast with a fiddler crab of the west coast. This study provides a behavioral basis for the electrophysiological data obtained on the visual fibers characteristics found in _U_. _crenulata_ and opens new horizons for research comparing neurophysiological results with behavioral observations in other _Uca_ species.

Unfortunately, all the questions relating to U. *crenulata* behavior could not be answered during the two-year period in which this research was conducted, as the method of observation used in this study did not permit observation of coupling. Since more research is needed concerning the mating behavior, I would suggest additional studies using consistent nocturnal observations with adequate illumination.

SUMMARY

1. Environmental factors such as soil consistency, topography and tidal pattern determine the presence of *U. crenulata* colonies.

2. The *U. crenulata* crab population of Carlsbad is formed by two distinct types of animals: a permanent group and a transient one. These two types of crabs differ by their feeding and mating behavior, and burrow structure.

3. A seasonal variation can be observed in the crab density on the surface, as well as in the male-female ratio.

4. A color variation from dark to light (in the permanent population) is associated with behavioral changes during the breeding season.

5. The behavioral activities are displayed only during low tide periods and varies according to seasons, temperature and light intensity.

6. The waving behavior typical to *Uca* species is observed in *U. crenulata* and shows two different types of wave: (a) a low frequency wave which can take place in absence of females and repeats itself with a cycle of 4 to 6.5 seconds; (b) a high frequency wave which is displayed only in presence of females and repeats itself with a cycle of 1 to 5 seconds.

7. The rate of the high frequency wave's major component corresponds to the optimum stimulus speeds (30 ± 3

degrees/second) of a rate sensitive neuron found in the optic nerve of the crab. This shows a strong relation between behavioral field data and physiological data concerning movement and rate selective neurons in the eye of the crab *U. crenulata*.

8. Nine different stages are identified in the egg development of *U. crenulata* and the time necessary to complete the incubation shows a breeding cycle length of two weeks.

9. The comparison of the tidal pattern of Oceanside with the identified breeding cycle suggests that *U. crenulata* females release their eggs during spring tides.

10. The typical mating behavior of the broad-front *Uca* described by Crane (1957) is absent in the *U. crenulata* colony of Carlsbad during the breeding season of 1981 and 1982. This suggests an adaptation of both males and females to a different pattern of mating.

APPENDIX

ACTIVITY	MATING PERIOD					NON-MATING PERIOD				
	time (hours)					time (hours)				
	1	2	3	4	5	1	2	3	4	5
EATING	40	30	10			80	75	50	20	10
WAVING		20	60	80	100					
IN BURROW	10	10	10	10		20	25	50	90	90
IMMOBILE	30	20	10	10						
BURROW BLDG	10	10	10							
FIGHTING	10	10								

Table 1. Behavioral activities of the crab colony during 1982, showing the percentage of crabs displaying during each hour of observation.

	J	F	M	A	M	J	J	A	S	O	N	D
PI(d)	100	100	100	92.7	65.6	31.6	30	31.6	94.3	99.5	100	100
PI(l)	0	0	0	37.4	75.5	94.9	95.4	94.9	33.2	10	0	0

Table 2. Population index for the dark and light male population for each month of the year 1982.

PI (d): dark male population index
PI (l): light male population index

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