

BEHAVIOURAL RESPONSES OF THE CRAB
HEMIGRAPUS OREGONENSIS TO TEMPERATURE,
DIURNAL LIGHT VARIATION, AND FOOD STIMULI.

BY

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ABSTRACT

Crabs of the species Hemigrapsus oregonensis, when held at temperatures of 5° and 18°C for eight days and then observed at temperatures approximating these holding conditions and at intermediate temperatures, showed greatest locomotor activity and frequency of behaviour patterns at highest temperature conditions. At intermediate temperatures, locomotor activity was greater in crabs from the higher holding condition, and the greatest variability was recorded for females at an observation temperature of 19°C. Observations made at 0530, 1030, 1630 and 2230 hours of the day showed that a peak activity period occurred at 0530 hours in male crabs at most temperature conditions. This may have been caused by the low intensity of illumination used at night.

Presentation of chemical food stimuli in the form of a solution of liver to crabs, elicited feeding and probing movements and an increase in locomotor activity. Pieces of art eraser simulating tactile stimuli of meat elicited feeding movements, but no response could be shown to sight of sculpins or minced liver. Visual stimuli appeared ineffective even when combined with other stimuli. Combinations of chemical and tactile

stimuli, however, appeared to sum, and responses were increased above those obtained by separate presentation. Starvation increased the frequency of all behaviour that occurred as a response to food stimuli.

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INTRODUCTION

Behavioural phenomena, like those of morphology and physiology, may aid the animal to survive, but to do so, the behaviour must be adapted to the environment and to changes that might occur in that environment.¹ The animal is limited in its distribution by a change in environmental factors, and by the extent to which the animal's morphology, physiology and behaviour can alter to adapt the animal to these changed conditions. To understand the limitations of an animal in its environment, a study of its behaviour and the adaptability of its behaviour is illuminating. Since a study of behaviour under all types of environmental change is clearly impractical, a few aspects considered to be important must be selected.

Environmental factors may be classed as biotic and abiotic. Abiotic factors may be exemplified by temperature, salinity, light and substrate, while biotic factors include the influences and effects of other animals, for example, competition for food, shelter, or a mate, and avoidance of predators. The behaviour of any successful animal must be adapted to all these, but to an extent varying between species and depending upon the particular habitat the species occupies.² To the shore crab Hemigrapsus oregonensis, abiotic factors of

temperature, salinity and light are important, since fluctuations in each of these factors occur in the intertidal habitat. Temperature alters the behaviour of some insects (Mellanby, 1939; Nicholson, 1934) and its effect on activities of poikilotherms is well known (Bullock, 1955; Prosser, 1955). The day-night light cycle has been shown to affect the chromatophore rhythm of fiddler crabs (Brown and Webb, 1939), and locomotor activity of cockroaches (Gunn, 1940). One effect of temperature or light was a considerable change in locomotor activity. Since activity is an integral part of all behaviour, knowledge of temperature and light effects on behavioural activity of H. oregonensis was considered basic to the investigation of behavioural changes caused by other alterations of the environment. Salinity effects have not been considered, and all behaviour work on this crab was carried out at a constant salinity.

Response to food stimuli is a behavioural characteristic affecting survival of an animal as a competitor for food. A classical experiment on stimuli and responses was that of Tinbergen and Kuenen (1939). They showed that gaping responses of nestling thrushes to various stimuli may have releasing and directing components. With respect to crabs, Hiatt (1948) investigated the response of Pachygrapsus crassipes to chemical,

tactile and visual food stimuli, but he was interested chiefly in discovering which senses were used by the animal. His field observations and experiments were not designed to distinguish between releasing and directing components of responses. Feeding behaviour, because of its ubiquity among animals, and its relation to the biotic factor of competition for food, was studied in H. oregonensis with special reference to the releasing and directing components of responses. Further, as competition increases with a decrease in availability of food, behaviour changes resulting from starvation also were considered.

Initially, a description of behaviour patterns of H. oregonensis was necessary as a means of describing and measuring the changes resulting from manipulation of the environment. Experiments demonstrating behavioural changes at different temperatures and light conditions as examples of abiotic factors, and with food stimuli and starvation as phenomena related to biotic factors, were then performed. Results permitted a discussion of the adaptability of behaviour of this crab, and demonstrated some behavioural mechanisms, such as release, direction, and summation of movements, which underly this adaptability.

MATERIAL AND METHODS

The shore crab Hemigrapsus oregonensis is an active animal displaying a diversity of behaviour, which, together with its abundance and ease of maintenance under laboratory conditions, makes the species well suited as the subject of an invertebrate behaviour study. "The species occurs as an inhabitant of the littoral zone from Prince William sound, Alaska, south to the Gulf of California. (Schmitt, 1921)."

HABITAT

At Spanish Bank, Vancouver, British Columbia, the collecting area for crabs used in this behaviour study, "the species occupies the lower intertidal areas from approximately the 3.0 foot to the 8.0 foot tide level (based on Pacific Coast Tide and Current Tables, Canadian Hydrographic Service, Department of Mines and Technical Surveys)". The Spanish Bank habitat is a mud-sand beach with outcrops of boulders extending down to the 3.0 foot tide level. Water temperatures fluctuate from approximately 5°C in winter to 20°C in summer, and the salinity at each of these seasons is approximately 75% sea water (based on 31.88‰ salinity, 17.65‰ chlorinity as 100% sea water) and 35% sea water in

winter and summer respectively.

The habitat provides abundant shelter and food. At times when the beach is exposed to air by the tide, most crabs seek cover beneath boulders. Marine algae Enteromorpha sp., Ulva lactuca and Fucus sp. may also be used as cover, and the first two algae may be used for food. The crab is omniverous and, besides algae, eats dead or damaged mussels, barnacles, worms, and may eat crabs of its own and the related species H. nudus. Chief predators of H. oregononensis in this area are probably gulls, raccoons and mink.

HOLDING CONDITIONS

Mature male and female crabs varying from 13 mm. to 25 mm. carapace width, were collected and brought to the laboratory where they were placed either in plastic trays (10.5" x 13.0" x 4.5"), or aquaria (8.5" x 14.0" x 10.0"). Both containers were filled to a depth of three or four inches with 75% sea water (25% salinity). A layer of sand approximately one inch deep covered the bottoms of aquaria, but sand was not used in the plastic trays. Crabs held in aquaria were used for observations describing movements and for experiments on temperature and diurnal effects; those held in plastic trays were used for experiments on feed-

ing behaviour. The use of two types of container was necessitated by methods of controlling holding temperatures. Plastic trays were kept in refrigerators, aquaria were kept either in water baths or at room temperature, depending on the control required.

Holding temperatures varied between experiments. Crabs used for observations describing movements, were held at room temperature, approximately 20°C. Two holding temperatures of 5°C and 18°C were employed for crabs used in experiments on temperature and diurnal effects. As a result of the data on temperature effects, a holding temperature of 15°C was selected for animals used in all subsequent experiments on feeding behaviour.

Salinity and photoperiod were constant throughout the work. Salinities of 75‰ sea water (25‰ salinity) were used, and a summer photoperiod of 16 hours light of approximately 20 foot candles was provided daily.

Crabs were fed raw minced beef liver each morning and sea water was changed daily. Animals held in plastic trays were cleaned by pouring off the fouled water together with any remaining food. Trays were then refilled immediately with fresh sea water. To clean the crabs held in aquaria, the dirty water was first siphoned or poured off, and sand and crabs were rinsed by pouring sea water quickly into the aquarium. This rinse water was then removed, and clean salt water sub-

stituted.

Crabs usually were kept 24 hours in the laboratory before being used in experiments to give them time to adjust to laboratory conditions. Animals were never kept over two weeks if they were to be used for experimental purposes. It was hoped these limits on holding periods would minimize any effects of laboratory conditions on behaviour. Crabs used for observations describing movements, were kept one month in the laboratory in which time few deaths and no noticeable change in physical condition or behaviour were observed.

OBSERVATION CONDITIONS

To record crab behaviour, pairs of crabs were placed in an observation container, which was usually partly immersed in a water bath to control temperature, and the observer made the recordings from behind a cardboard screen which was provided with slits to permit viewing. Size and shape of the observation container varied between experiments, but there was always a layer of sand one inch deep covering the bottom, and the container always was filled with sea water to a depth of three or four inches. Salinity was approximately 75% sea water (25% salinity). Crabs always were observed in pairs and in each experiment, as nearly equal numbers

of males and males, males and females, and females and females, were used as possible. Females with eggs were never used for observation purposes.

Behaviour was recorded by the use of abbreviations or symbols distinctive for each behaviour pattern. A symbol was written each time behaviour changed from one pattern or type of movement to the next. Groups of similar movements or "bouts" therefore were recorded by one symbol, and were indistinguishable from the recording of a single movement. Recordings were made in five minute block intervals, but this interval was found to be too short, and the frequency of bouts was calculated for the entire length of each observation period. Observation periods were usually ten or fifteen minutes in length depending on the experiment.

Before observations were begun, a period was allowed for adjustment of the animals to the observation situation. The length of this settling period, and factors such as temperature and light, changed according to the aspect of behaviour being studied. Details of these conditions are presented with the description of experimental design.

EXPERIMENTAL DESIGN

Behaviour work on Hemigrapsus oregonensis is

divisible into three parts: (1) Description of Movements (2) Temperature and Diurnal Effects, and (3) Feeding Behaviour. The third part can be subdivided further into (a) an investigation of responses to food stimuli and (b) effects of starvation on feeding behaviour. The experimental design for each of these parts is described separately.

1. Description of Movements:

Pairs of animals in all combinations of sexes were observed in a 12 by 24 inch aquarium. The observation periods were one hour in length and a total of 60 observation hours was recorded. The water temperature was approximately 20°C, and the illumination approximately 20 foot candles. These observations provided a description of the behaviour patterns or movements used in all subsequent experiments.

2. Temperature and Diurnal Effects:

This experiment was designed to study the effects of holding and observation temperatures, and effects of relatively bright illumination during the day, and low illumination at night on locomotor activity and frequency of behaviour patterns. Locomotor activity was measured by recording the distances the crabs moved around the observation container. Animals were numbered

with a wax pencil so that every individual could be distinguished, and then were divided into four groups of 6 crabs per group. Two of the four groups were held for eight days at 5°, and the other two groups for eight days at 18°C.

Temperature effects were measured by making observations at three temperature conditions. One group from each holding temperature was observed at a temperature approximating its own holding condition (observation temperatures 7° and 19°C). The remaining two groups, one from each holding condition, were observed at intermediate temperatures of 10° and 11°C. The difference between these two intermediate temperatures was considered negligible. The arrangement of temperature conditions is shown in Table I.

Diurnal effects were studied by conducting observations on all temperature groups at four times of day. These times were 0530, 1030, 1630 and 2230 hours. Illumination at 1030 and 1630 hours ranged from 17 to 25 foot candles, and illumination during night observations at 0530 and 2230 was one-half foot candle. Animals were rotated so that every individual was observed at each time of day.

The experimental design is given in Table I, and the entire procedure was run twice, using the same animals, to give a total of 192 observation periods of

TABLE I

Holding Temperature: 5°C. Day 1 Day 2 Day 3
 Observation temperature: 7°C.

Time:	0530	♂10	♂11	♂20	♀14	♀9	♀10
	1030	♀9	♀10	♂10	♂11	♂20	♀14
	1630	♂20	♀14	♀9	♀10	♂10	♂11
	2230	♂10	♂11	♂20	♀14	♀9	♀10

Holding temperature: 5°C
 Observation temperature: 11°C

Time:	0530	♂4	♂7	♂15	♀8	♀6	♀7
	1030	♀6	♀7	♂4	♂7	♂15	♀8
	1630	♂15	♀8	♀6	♀7	♂4	♂7
	2230	♂4	♂7	♂15	♀8	♀6	♀7

Holding temperature: 18°C
 Observation temperature: 10°C

Time:	0530	♂18	♂20	♂10	♀11	♀14	♀15
	1030	♀14	♀15	♂18	♂20	♂10	♀11
	1630	♂10	♀11	♀14	♀15	♂18	♂20
	2230	♂18	♂20	♂10	♀11	♀14	♀15

Holding temperature: 18°C
 Observation temperature: 19°C

Time:	0530	♂11	♂12	♂19	♀13	♀9	♀10
	1030	♀9	♀10	♂11	♂12	♀19	♀13
	1630	♂19	♀13	♀9	♀10	♂11	♂12
	2230	♂11	♂12	♂19	♀13	♀9	♀10

fifteen minutes each. The settling period preceding observation, was one hour. Plastic boxes (7.5" x 5.5" x 3.5") were used as observation containers.

3. Feeding Behaviour:

Responses to Food Stimuli

The results of Hiatt's field experiments on reactions of Pachygrapsus crassipes to chemical, visual and tactile food stimuli suggested a similar investigation should be carried out on Hemigrapsus oregonensis in the laboratory. Two types of experiment were employed to test responses to food stimuli. Time Control experiments compared behaviour during control periods in absence of food stimuli with stimulus periods in which stimuli were present. These experiments tested releasing components of food stimuli. Directing components were demonstrated by means of choice experiments in which behaviour at the two ends of the container was compared. The two ends differed; food stimuli were presented at one end but not at the other. Settling periods before the start of observations were one-half hour in length for both types of experiment, and a temperature of 15°C and illumination of 5 foot candles were used throughout. All experiments on feeding behaviour were performed between the hours of midnight and 0400, as results of the preceding experiment showed crabs were probably most ac-

tive during these hours.

Procedure and conditions for Time Control and Choice experiments differed in some respects. In Time Control experiments, the observation period was divided into a ten minute control period followed immediately by a ten minute stimulus period. Observation aquaria 8.5 by 14.0 by 10.0 inches were used. Releasing components of chemical, tactile, and combined chemical and tactile, visual and tactile, and visual, chemical and tactile stimuli were studied by means of this type of experiment.

In Choice experiments, observation periods were fifteen minutes in length, and the observation container consisted of a tripartite box (7.5" x 5.5" x 3.5"). The three compartments of this box were separated by watertight, transparent plastic screens when visual stimuli were being investigated, and by a porous plastic screen wrapped in cheese cloth for investigations of chemical stimuli. Directing components of visual stimuli, and the directing components of visual stimuli in the presence of non-directing chemical stimuli were investigated by means of Choice experiments.

The combinations of stimuli together with some of the conditions of each experiment are presented in Table (11). Methods of presenting various stimuli to the crabs are described below.

*Revised
November 11*

Chemical Stimuli: An extract or solution of the raw minced beef liver normally used for feeding was prepared by stirring 10 grams of the liver in 400 ml of sea water. For Time Control experiments, this preparation was allowed to settle ten minutes before the solution was decanted into a supply aquarium filled with approximately half a gallon of sea water. The liver solution or chemical stimulus, was siphoned to the observation aquarium during the ten minute stimulus period. During the control periods of this experiment (Time Control experiment 1, Table 11), ordinary 75% sea water was siphoned into the observation aquarium. Thus, presence or absence of chemical stimuli, and the depth of the water were the only factors changing between the control periods and the stimulus periods. Depth, however, increased at a constant rate throughout the experiment.

× Directing components of chemical stimuli were studied by means of a Choice experiment (Choice experiment 3, Table 11). The tripartite observation box was provided with porous opaque screens partitioning off the two ends of the container. Ten grams of liver were dropped into one of the end compartments, and observations were begun immediately.

× Chemical stimuli were employed as a releasing component, and visual stimuli as a directing component in Choice experiment 4 (Table 11). Chemical stimuli were

TABLE II

Showing the types and some of the conditions of experiments on responses to food stimuli.

TYPE OF EXPERIMENT	NO	STIMULUS COMBINATIONS	STIMULUS OBJECTS	CONDITION OF CRABS	LENGTH OF OBSERVATION PERIOD
TIME CONTROL EXPERIMENTS	1	Chemical	Liver Extract	normal	10 minutes control period followed by 10 minutes stimulus period.
	2	Tactile	Gum eraser	blinded	
	3	Visual & Tactile	Gum eraser	normal	
	4	Chemical & Tactile	Liver extract & Gum eraser	blinded	
	5	Visual, Chem. & Tactile	Liver extract & Gum eraser	normal	
CHOICE EXPERIMENTS	1	Visual	Raw minced liver	normal	15 minutes
	2	Visual	Sculpin	normal	
	3	Chemical	Raw minced liver	normal	
	4	Visual choice Chem. excitatory	Raw minced liver and liver extract	normal	

presented by decanting the liver extract straight into the center compartment containing the crabs. The extract and sea water became mixed in a few seconds, and any differences in behaviour of the crabs at either end of the observation container, must have been caused by the visual stimuli.

Tactile Stimuli: Tactile stimuli were presented by dropping ten pieces of gum eraser into the observation aquarium. Gum eraser was chosen as a stimulus object because the eraser has a soft but firm consistency not unlike meat, and is not accompanied by chemical stimuli associated with meat. In experiments where visual stimuli were to be eliminated (Time Control experiments 2 and 4) the animals were blinded. Blinding was performed by coating the eye-stalks with plastic aluminum. This substance dried fairly hard in air within half an hour of application, and appeared to cause no ill effects to the crab or its eyes. Blinded crabs were allowed at least 24 hours to readjust before being used in feeding experiments.

Results from experiments with tactile food stimuli should probably be interpreted with caution, as gum eraser has specific qualities of its own to which the crabs might have been reacting, rather than to the simulated qualities of meat. The possibility that crabs might have been reacting to chemical stimuli from the

eraser also cannot be ignored.

Visual Stimuli: To present visual food stimuli alone, chemical and tactile food stimuli had to be eliminated from the environment. This was accomplished by separating the crabs from the food with a watertight transparent screen. To insure crabs reacted to the food rather than to an asymmetrical observation container, the tripartite observation box already described, was designed. Crabs were placed in the center compartment and the object used as a visual stimulus was placed in one end. Ends were used alternately on repeated trials.

Two different visual stimulus objects were employed. Ten grams of raw minced liver were used for one set of observations (Choice experiment 1), but because of its shapelessness and lack of movement, liver was felt to be unsatisfactory. A second set of observations were run using a tidepool sculpin (Oligocottus maculosus). These small fish have definite form and are continually moving their gill operculi, thus overcoming both disadvantages of liver. Though H. oregonensis has not been observed eating sculpins, omniverous habits of the crab suggest these fish might be used as food.

No special procedure was followed in experiments where visual stimuli were presented in conjunction

with tactile or tactile and chemical stimuli (Time Control experiments 3 and 5), except that crabs were not blinded. This permitted the animals to see as well as feel the pieces of gum eraser used as tactile stimulus objects. The light coloured pieces of gum eraser were easily visible on the sand and were probably as visually distinctive as most objects eaten by the crab.

Combined Stimuli: When tactile and chemical stimuli were presented in combinations, the method of presentation of each stimulus followed the procedure used when presenting each type of stimulus by itself. Visual stimuli in combinations with tactile stimuli were presented by leaving crabs unblinded, as described. The method of presenting chemical stimuli as an excitatory factor with vision as the directing stimulus (Choice experiment, 4) was described in the section on chemical stimuli.

Each experiment was replicated ten times, individual crabs never being used more than once. As two crabs were observed at a time, the sample size for each experiment was twenty.

Data from control and stimulus periods were compared by subtracting figures in control periods from the figures obtained during stimulus periods or, in the case of Choice experiments, numbers of move-

ments recorded on the side of the container without the stimulus were subtracted from numbers recorded on the side nearest the stimulus. Data for any observation periods in which the crabs remained completely inactive, were discarded and the observations repeated. Completely inactive crabs could not demonstrate differences in behaviour, and data from these observation periods could only serve to obscure differences that might actually be present. Exclusion of these data, therefore is justified.

Effects of Starvation

The effects of starvation on feeding behaviour were investigated by starving crabs for two arbitrary periods of time, and then observing their behaviour in the presence of chemical, tactile, and combined chemical and tactile food stimuli. Starvation periods of five days and ten days were chosen. Before the starvation periods began, animals were held two days in the laboratory under normal holding conditions, including the daily feeding with raw minced beef liver. These two days were intended as an equilibration period to ensure that every crab at least had the opportunity to feed before starvation was started. During the starvation periods, holding conditions were unchanged except that feeding was omitted.

Presentation of stimuli followed methods al-

ready described. Chemical stimuli were presented by siphoning liver extract to the animals during the stimulus period under the same conditions given for Time Control experiment 1 in Table II. Tactile stimuli were presented by means of the gum eraser which was used to simulate meat. As results from the experiments on responses to food stimuli indicated vision had little or no effect on feeding behaviour, use of blinded crabs was not considered necessary. Tactile stimuli in starvation experiments were presented in the manner described for visual and tactile stimuli in the preceding section (Time Control experiment 3, Table II). Chemical and tactile stimuli were combined by presenting pieces of gum eraser and liver extract simultaneously. Conditions were equivalent to those described for the experiment on response to visual, chemical and tactile food stimuli (Time Control experiment 5, Table II).

Data from experiments investigating responses to food stimuli and experiments on starvation were comparable, because observation procedures used in the two sets of experiments were similar. Crabs used in the investigation of responses were fed daily, and cleaned six hours previous to being used for observations. Accommodation of sense organs to presence of food presumably disappeared at the end of this six hour period in clean water. Inclusion of these data with data from

starvation experiments gave figures for behaviour responses to food stimuli at zero, five and ten days starvation.

ANALYSIS OF BEHAVIOUR

The analysis of behaviour used in this work was designed to describe changes in behaviour occurring in a given time period. Three types of measurement can be made. For each behaviour pattern investigated, these measurements are: (1) the total time spent performing that pattern, (2) the mean length of bouts (a bout being a sequence of one behaviour pattern only) and (3) the number of bouts occurring per time unit. These methods are not independent, as the measurement given by any one, can be derived if measurements from the other two methods are known. For instance, the mean length of preening bouts of a bird can be calculated if the number of preening bouts and the total time spent preening have been recorded.

Behaviour of H. oregonensis was described by measuring the number of bouts of each movement. Each time a crab changed from one behaviour pattern to the next, the new behaviour pattern or movement received a value of one; repetitions of a movement were disregarded.

Neither mean lengths of bouts nor total time spent on each movement were recorded. This procedure had the advantage of permitting recording of two animals at once, but the use of numbers of bouts as a measurement of behaviour also has disadvantages. These disadvantages are discussed by Cane (1961).

Cane (op. cit.) points out that the number of bouts occurring in a given time period is few when the behaviour pattern occurs rarely, and is also few when the behaviour pattern occurs very often. If the proportion of bouts of one behaviour pattern is raised with respect to the others, and if the sequence of performance of behaviour patterns is random, then the probability of two bouts of the same type occurring together increases. The mean length of bouts is increased, therefore, but the recorded number of bouts is decreased correspondingly. Cane shows that a maximum number of bouts occurs when the behaviour pattern under consideration occupies about half (50%) of the time of observation. The question arises: are low numbers of bouts describing the behaviour of H. oregonensis indicative of a small quantity of that behaviour, or a large quantity? Bouts of all behaviour patterns, with the exception of standing and crouching, were of short duration, seldom lasting more than a few seconds each, and often consisting of only one completed motion. Bouts were

separated in most cases by a pause which was recorded as a stand or a crouch. Thus, of all behaviour patterns occurring per time period, at least 50% of them were standing or crouching movements. Feeding bouts, even when occurring at their maximum frequency, comprised only 9% of all behaviour patterns recorded in the observation period. Each feeding bout would have to be extremely long before this low frequency could be considered an indication of a great quantity of feeding. Standing and crouching were the only behaviour patterns maintained without interruption for several minutes or even hours.

The assumption, then, that the number of bouts of any behaviour pattern (except standing and crouching) can be used as a direct measure of the frequency of that behaviour, is considered to be justified. The behaviour of H. oregonensis can be satisfactorily described in terms of the number of bouts of various movements per time unit.

STATISTICAL ANALYSIS

(1) Temperature and Diurnal effects: The statistical significance of differences in locomotor activity of the two sexes at holding and observation temperatures was calculated by analysis of variance

given in Tables III, IV, and V. The effect of temperature on frequency of behaviour patterns was analyzed by means of a four by three Chi-square test. Frequencies of some movements when considered individually were too small for analysis, and in order to increase the size of numbers, various movements were grouped. In spite of this, one "expected" cell frequency was still less than 5. According to Snedecor (1956) "if the frequency observed in any cell is less than 5, close decisions may be affected!" The probability calculated from figures in Table VI was less than 0.001, which cannot be considered a close decision when the usual probability value accepted was 0.05 or less. The results of the Chi-square test were therefore accepted as being significant.

The frequencies of all behaviour patterns except digging were too few to analyze for variation at different times of day. A difference in digging frequency was examined by means of "Student's" t-test.

(2) Responses to Food Stimuli: A nonparametric Binomial test for small samples (Siegel 1956) was used to test significance of feeding responses. However, the test does not measure the significance of the figures presented in Table VII where probability values are indicated. The test compares the number of observations in which the response was positive with

the number in which the response was negative, and the level of probability refers to the significance of numbers of observations showing a positive response.

The level of probability (P) accepted as being significant was 0.05. Higher levels of significance have been indicated where they occurred.

RESULTS

DESCRIPTION OF MOVEMENTS

Observations were first made to describe basic behaviour patterns or movements of the crab Hemigrapsus oregonensis. Evidence has been presented where possible to support the conclusions concerning the function of each movement. Names of movements were chosen to imply function where that function appeared to be self evident, eg. "feeding", "washing". Where the function was doubtful, names were chosen to avoid implications, eg. "claw-wave", "creaking", and "snatching". Separate behaviour patterns with the same function received the same name. Each of the three types of digging, for instance, was described under the name "digging". Related movements were grouped in the presentation of results of later experiments.

Walking: Crabs normally walk sideways, although

for short distances a crab may move directly forwards or backwards. The body is held off the ground, except when moving slowly, at which time it may or may not be touching the sand. Occasionally, a crab may make a short dash towards or away from another crab, but advances or retreats are usually intermediate in speed. Crabs seldom move away from the wall of the aquarium. This habit simplifies measurement of distance travelled per time unit, as the animal's movement along a side of the aquarium can be accurately recorded.

Climbing: Climbing consists of raising the legs on one side of the animal up the side of the aquarium (Fig. 1A). While in this position, the crab may sidle along the wall of the tank, or attempt to crawl up the aquarium cement in a corner.

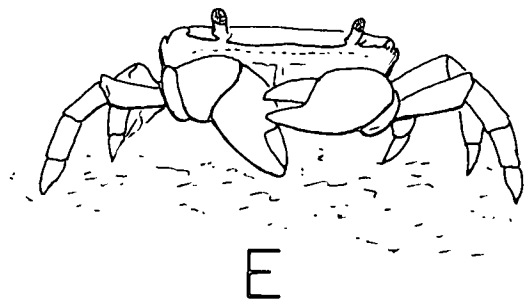
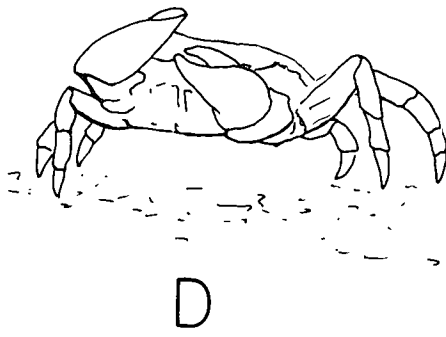
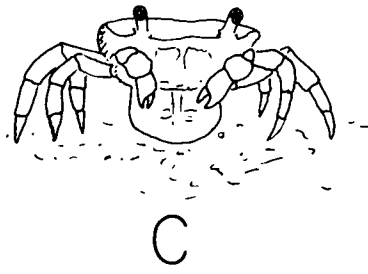
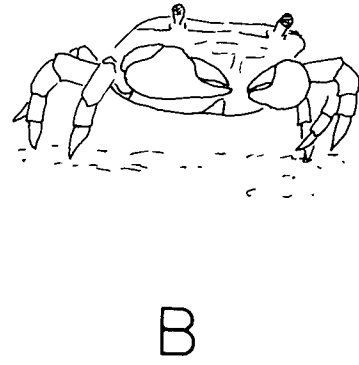
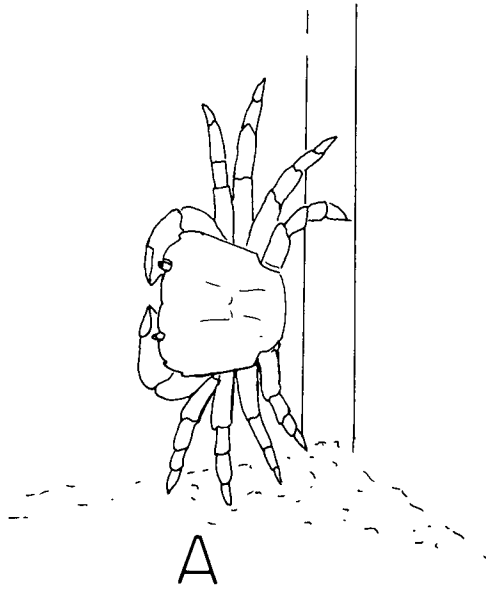
Standing and Crouching: These two postures differ only in the height the body is held above the ground. Abdomen and thorax rest on the sand in the crouch posture, and are raised off the ground when the animal is standing. One posture is not preferred to the other by a particular crab, nor does either appear to signify attitudes of dominance or submission. A stand or crouch was recorded when a crab was momentarily motionless, with the chelipeds in the normal carrying position parallel to the front of the crab (Fig. 1B).

Abdomen flapping: A standing crab raises and

Figure 1.

Some behaviour patterns of H.oregonensis
are shown

- A. Male crab climbing
- B. Male standing with claws in normal carrying position.
- C. Female abdomen flapping, showing clipping movements in region of abdominal appendages.
- D. Male washing, rubbing front of carapace with claws.
- E. Male washing, making clipping motions at one claw with the other.



lowers the abdomen two or more times in succession. This movement is frequently made by females, but seldom by males, which suggests an association with female reproductive or parental behaviour. When females are carrying eggs on the abdomen, the motion would increase water flow, aiding the respiration of the embryos.

Also classed as abdomen flapping are cases where the abdomen is lowered and kept in the extended position while clipping movements with the claws are made in the region of the abdominal appendages (Fig. 1C). Removal of faeces by the claws has been observed during this procedure, which suggests this movement could be classed as "washing". Both types of abdomen flapping are rare, and neither has been used in the analysis of behaviour.

Hiatt (1948) has observed similar movements of the abdomen in Pachygrapsus crassipes. He reports the movement was observed most frequently in both males and females during and immediately after copulation.

Washing: Washing movements include a variety of distinct motions. The claws may be rubbed over the front of the carapace (Fig. 1D), mouthparts, and sometimes ventral surfaces of the crab. One of the claws may be used to make clipping movements at the same areas, or at the surface of the opposite claw (Fig. 1E).

The legs also may be rubbed one against the other. All these movements apparently function to cleanse the surface of the animal.

Probing: Results of experiments with food stimuli, described later, suggest this movement is a part of appetitive feeding behaviour. The claws probe in the sand as if searching for food, but are not moved to the mouth.

Feeding: This movement is performed both in the presence and absence of food. When food is absent, the claws probe in the sand, but consequently are moved to the mouthparts (Fig. 2A), distinguishing this movement from probing. When present, food may be held in one claw while the other is used to tear pieces off and pass them to the maxillipeds, or both claws may be used to hold the food, and the maxillipeds are used for tearing.

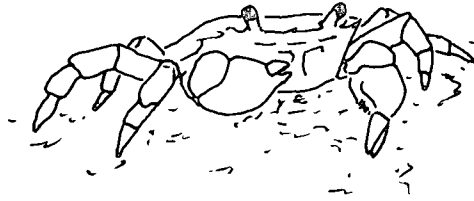
Claw-waving: A crab may raise its claw as it approaches or is approached by another crab (Fig. 2B). The movement comprises raising and extending the claw from the normal carrying position parallel to the front of the crab, to a position approximately at right angles to the front. The dactylus is partly open. The claw may be held in the extended position for a moment, or may be lowered immediately.

While this movement was not investigated sys-

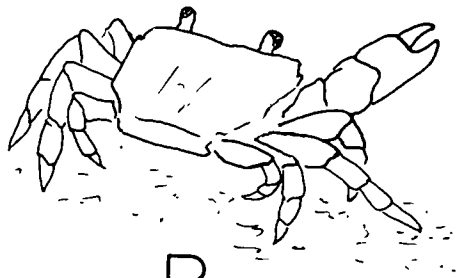
Figure 2.

Behaviour patterns of H. oregonensis.

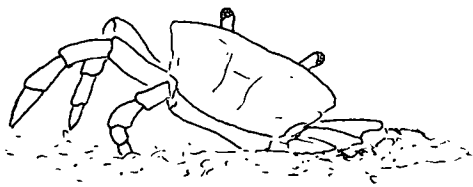
- A. Male feeding.
- B. Male claw-waving
- C. Digging. Legs of one side
are buried in the first phase
towards burial of the entire
animal in the sand.
- D. Digging. The right claw is
being used as an implement for
shovelling sand.



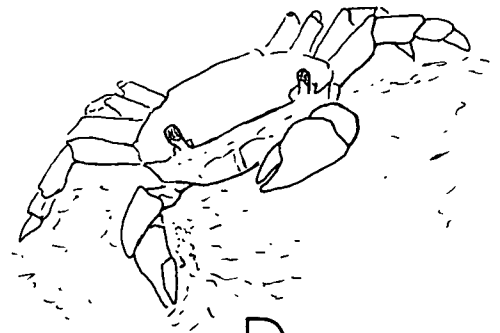
A



B



C



D

tematically, some evidence of its function is presented. Figure 3 shows the proportions of advances and retreats of a "waved at" female crab before and after the waving movement, compared with the movements of a crab before and after climbing motions of a nearby animal. Though climbing is a more conspicuous movement involving the whole crab rather than a part, claw-waving is followed by a greater number of retreats. This suggests claw-waving could function as a threat movement; it may prohibit the approach of other animals without incurring a fight.

Claw-waving of Uca differs from that of Hemigrapsus. Uca extends the claw horizontally, and while holding it in this position may give a jump or jerk before raising the claw vertically (Gordon, 1958). The claw is lowered in a series of distinct jerks in some species, while in others it is lowered smoothly (Crane, 1943). No comparable beckoning motion is made by Hemigrapsus. Crane (1957) claims claw-waving by fiddler crabs may function as a non-sexual territorial, or sexual territorial movement, a sex attractant, and a challenge to other males. All these functions may occur in one species, but more often do not.

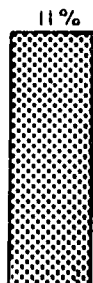
Aufbaum reflex (Bethe, 1897): The crab stands high on its legs, the claws extended and raised, with the dactylus open. This is the posture adopted by the animal when one finds it on the beach some dis-

Figure 3

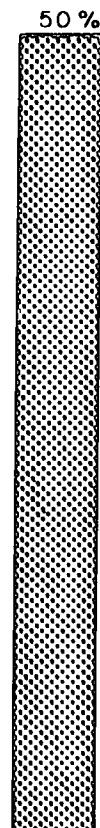
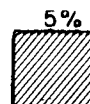
Relative change of advances to retreats
measured as a percentage of all movements:
A, before another crab claw-waves, and B, after
it claw-waves; C before another crab climbs, and
D, after it climbs. Figures were calculated from
a total of 78 claw-waves, and 200 climbing move-
ments.

PER CENT OF ALL MOVEMENTS

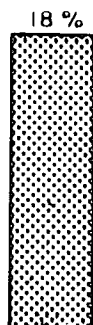
A



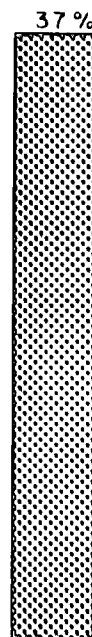
B



C



D



ADVANCES

RETREATS

ADVANCES

RETREATS

WALKING

MOVEMENTS

tance from cover. The posture appears to be a defence attitude towards predators. The aufbaum reflex has been described for the crabs Carcinus maenas (Bethe, 1897), Pachygrapsus crassipes (Hiatt, 1948) and Ocypoda (= Ocypode) arenaria (Cowles, 1908).

Sterrkampf reflex (Bethe, 1897): The ster-
rkampf or death feigning reaction occurs in some species of crabs when they are suddenly exposed by overturning a rock. The crab remains motionless even if handled. This response has been observed by Hiatt (1948) in Hemigrapsus nudus, but seldom if ever in H. oregonensis, and never in Pachygrapsus crassipes. Personal observations made while collecting crabs at Spanish Bank, confirm Hiatt's conclusion concerning H. oregonensis.

Digging: Three types of digging can be distinguished. First, the crab may crouch, and in this position work the legs of both sides into the sand simultaneously. The tips of the legs become buried in the sand, but the rest of the crab remains exposed. The second type is characterized by digging by the legs of one side into the sand first (Fig. 2C). This is followed by digging by the legs on the alternate side, and by pushing the back of the carapace into the sand. The entire crab may become buried, or digging may stop before the crab is covered completely. The third type

of digging consists of moving sand from one place to another by using the claw as a shovel (Fig. 2D). The crab moves the claw out to an angle at right angles to the front of the body, and lowers the claw into the sand. In this position the crab walks two to three inches, scooping sand along with the lowered cheliped. The operation may be repeated several times starting at the same location until a hollow large enough to accommodate the whole animal is dug. This method of digging is probably used to excavate a hole beneath rocks that have sunk into the sand on the beach. Similar sand digging movements have been described for the crab Ocypoda (=Ocypode) ceratophthalma as the method used in digging its burrow (Cott, 1928).

Snatching movements: From the normal carrying position, the claws are extended forward and brought rapidly together in a snatching or grabbing motion. The movement was observed to be directed always toward another crab or towards the bubbling air-breaker, and was usually preceded by a dash toward these objects.

Evidence concerning the function of this movement suggests two possible alternatives, neither of which are completely satisfactory. At first, the movement was thought to be a part of feeding behaviour, because the frequency of snatching movements made by a group of crabs increased upon the inflow of water con-

taining a solution of liver extract. However, the action could be elicited visually from two crabs separated by a clear plastic screen, and appeared to be directed by vision. The use of vision cast doubt on the hypothesis that feeding was the function of this movement, as later experiments were unsuccessful in demonstrating the use of vision in feeding. The second alternative, that the movement is a part of reproductive behaviour, is supported by the observation that copulation attempts frequently followed the capture of a female by snatching movements of a male. Only males have been observed to perform this action. However, this hypothesis unfortunately fails to provide a satisfactory reason for the rise in frequency caused by the liver extract. Possibly the movement functions as a general catching action, serving to procure food or a mate as the occasion demands.

Creaking: The body of the crab rocks forward on the legs and the claws are extended simultaneously, with the dactylus closed. This seemingly unbalanced posture is illustrated in Figure 4 A. Without pause, the preparatory phase is followed by movement of the claws outwards from the mid-line of the animal in a jerking or shuddering motion (Fig. 4B). The animal then returns immediately to the normal standing or crouching position. The movement is constant in speed and degree,

is conspicuous to an observer watching a group of animals, and the shuddering action of the claws is easily felt by anybody holding a crab when the movement is performed.

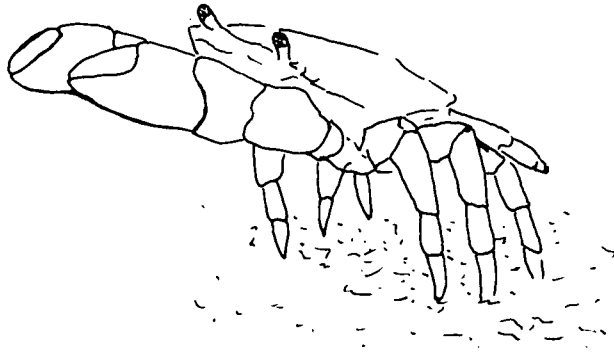
Creaking, like the snatching movement, is restricted to males and probably functions to prevent copulation attempts between two males crabs. A crab may perform the movement if mounted, held, or even touched by another crab. Creaking of one male is usually sufficient to cause the other male to climb off or let go. Male crayfish, which apparently have no such inhibitory motion, are reported to tear off each other's legs and antennae in attempts to copulate with one another (Scott, 1958).

Copulation: The process of copulation can be subdivided into three phases: the pairing of male with female, arrival of the pair at the correct copulatory position, and transfer of sperm. The male takes the active roll in selection of a mate, but the method of selection is by trial and error. Any crab over which a male happens to walk, or which is caught by a snatching movement, may be mounted. Mounting is accomplished by walking or crawling onto the carapace of a second crab, and gripping the carapace firmly with the feet. If the crab mounted is another male, it performs a creaking movement, and separation usually follows. Some-

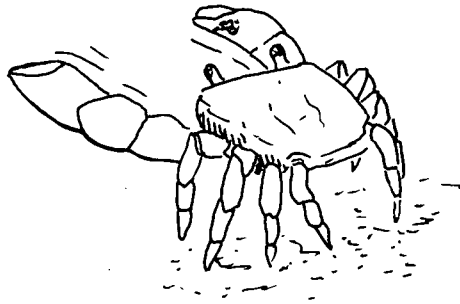
Figure 4.

Behaviour patterns of H. oregonensis.

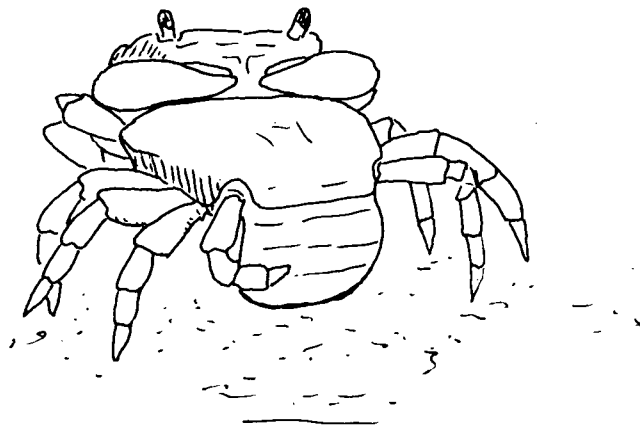
- A. Male, showing off balance posture at the start of creaking.
- B. Male creaking. The claws are moved apart in a shuddering motion.
- C. Male and Female in precopulatory position. The male is backing over the front of the female, preparatory to hanging upside down beneath her.



A



B



C

times escape is effected only with a struggle. Females when mounted either stand passively, or struggle free if not prepared to copulate.

Once pairing and mounting have been accomplished, the male is ready to maneuver to the copulatory position. If the male is not already facing the posterior of the female, and he usually is not, he turns around. Then, while the female stands passively, the male backs over her front (Fig. 4C). Both crabs keep their claws flexed, and seldom use them for holding. As the male comes beneath the female, each crab extends its abdomen, and the copulatory organs are joined. The male hangs upside down beneath the female, his legs inserted between hers gripping her carapace. Sperm is transferred to the female from this position.

Two points differ in this and the description by Hiatt (1948) of copulation in Pachygrapsus crassipes. Copulating female H. oregonensis were in the hard shelled C intermoult stage, whereas female Pachygrapsus were in the soft shelled A₁ intermoult stage. Secondly, copulation of H. oregonensis lasted only two to three minutes; copulation of Pachygrapsus on the other hand, lasted five to forty-five minutes. The edible crab, Cancer magister, may remain in a clasping position for a period of hours (McKay, 1943). Observations of copulating H. oregonensis were facilitated by discovery

that large numbers of crabs could be kept in one tank and excited to increased breeding activity by the procedure of cleaning the aquarium described earlier.

Compensatory eye-stalk movements: Tilting H. oregonensis to the right or left causes the uppermost eye to retract into its socket, and the lower eye stands erect. Tilting the crab forward causes both eyes to retract; tilting backwards results in both eyes erecting to the upright position. Pachygrapsus crassipes shows identical reactions to tilting (Hiatt, 1948), but Ocypode arenaria reacts oppositely when tilted to the side (Cowles, 1908). Ocypode arenaria retracts the lowermost eye when descending its burrow, the upper eye remains erect. Cowles (op. cit.) claims this reaction avoids the danger of breaking off the lowermost eye against the roof of the burrow, and leaves the uppermost eye, nearer the entrance of the burrow in a position permitting observation of predators.

Movements of antennae and antennules: The antennae can be retracted into sockets in the front of the carapace. The antennules keep up a continuous flickering movement, ceasing completely only upon death of the animal. Further examination may show antennule movement can be used as a measure of response to low level stimuli.

Respiratory movements: Continuous fluttering

of the scaphognathite causes a current of water to flow over the gill surfaces, and the gills are cleaned of sediment by movements of the mastigobranch. Movements of the gill bailer and mastigobranch are difficult to observe without dissection.

Of all movements described, only the following were used as measures of behaviour in subsequent observations: standing and crouching, climbing, washing, probing, feeding, claw-waving, digging and snatching.

TEMPERATURE EFFECTS

The effects of temperature on general locomotor activity of crabs are shown in Figure 5, and the statistical significance of differences appearing in this figure are shown by analyses of variance, Tables III, IV, and V. Holding temperatures were equally as important in their effects as observation temperatures. Comparison of activity of crabs held eight days at 5° and 18°C, but observed at nearly equal observation temperatures of 11° and 10°C respectively, showed that animals from the higher holding temperature were more active than those from the lower holding temperature. This difference was significant ($P < 0.01$, Analysis of variance Table III).

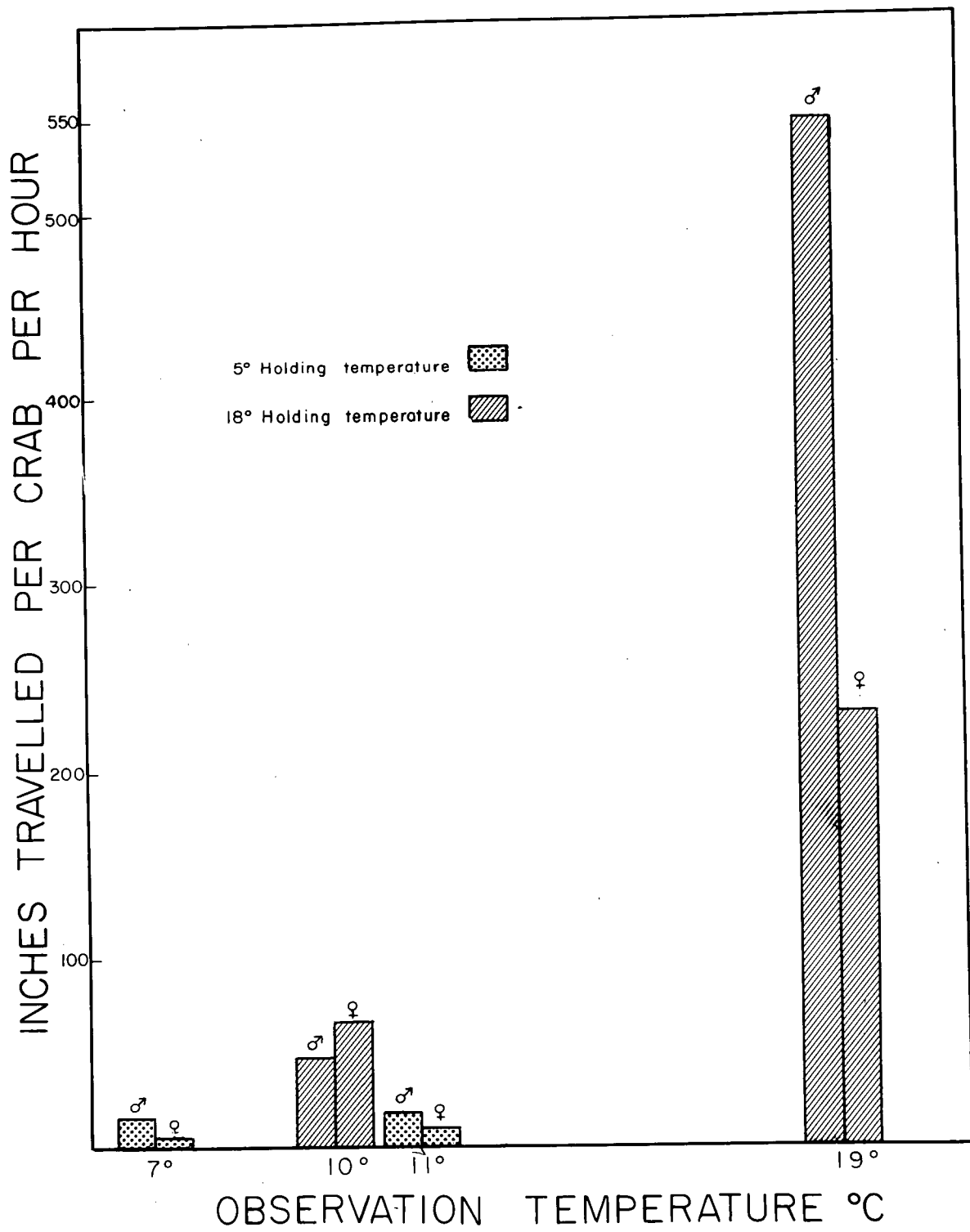
The effects of observation temperatures were

shown by comparing behaviour of animals held at one temperature and observed at two different temperatures. Crabs held at 5°C, for instance, showed almost identical levels of activity at 7° and 11° C observation temperatures, and the small differences that occurred were not significant (Analysis of variance, Table IV). Crabs held at 18°C showed a difference in activity level when activity was measured at observation temperatures of 10° and 19°C. A drop in temperature from 18° holding temperature to 10°C at observation conditions significantly lowered activity ($P < 0.01$, Analysis of variance, Table V).

These data warrant the following conclusions: (1) in general, locomotor activity is greater at higher temperatures than at low temperatures and (2) either the high activity caused by a high holding temperature is retained after a drop of 8°C for a period longer than one hour (the equilibration period), or the depression of activity caused by low holding temperatures is retained at least one hour after animals have undergone a rise of 6°C (5° holding temperature to 11° observation temperature), or both retention of high activity from high temperatures and low activity from low temperatures occur simultaneously. Additional data on crabs held and observed at the intermediate temperatures of 10° and 11° C are needed to decide between these

Figure 5

The effect of observation and holding temperatures on inches travelled per crab per hour. Each bar is calculated from a total of 18 fifteen minute observations on 3 crabs.



ANALYSIS OF VARIANCETABLE III

Observation Temperature intermediate (10° and 11°C). Effect of 5° and 18°C holding temperatures and sex on distance travelled (in inches)

Source of Variation	Sum of Squares	Degrees of Freedom	Variance Estimate	F Ratio
Temperature	2145	1	2145	11.47
Sex	39	1	39	0.21
Residual	12916	69	187	----
Total	15100	71	----	----

Locomotor activity is higher in crabs held at 18°C,

$P < 0.01$

Differences in locomotor activities of sexes is not significant, $P > 0.05$.

ANALYSIS OF VARIANCETABLE IV

Holding temperature 5°C. Effects of 7° and 11°C observation temperatures and sex on distance travelled (in inches)

Source of Variation	Sum of Squares	Degrees of Freedom	Variance Estimate	F Ratio
Temperature	25	1	25	0.52
Sex	85	1	85	1.77
Residual	3305	69	48	----
Total	3415	71	--	----

Difference in locomotor activity at 7° and 11°C
not significant, $P > 0.05$.

Difference in locomotor activity between sexes
not significant, $P > 0.05$.

TABLE V

Holding temperature 18°C. Effect of 10°C and 19°C observation temperatures and sex on distance travelled (in inches)

Source of Variation	Sum of Squares	Degrees of Freedom	Variance Estimate	F Ratio
Temperature	124251	1	124251	48.82
Sex	24976	1	24976	9.81
Residual	175613	69	2545	----
Total	324840	71	----	----

Locomotor activity is higher at 19°C,

$P < 0.01$.

Locomotor activity of males is greater than that of females, $P < 0.01$.

alternatives.

Temperature affected locomotor activity of the two sexes differently. Disparities in activity level between sexes at 7°C, 10°C, and 11°C were insignificant ($P > 0.05$, Analysis of variance, Tables III and IV). At 19°C observation temperature, however, the disparity became large, activity of males increased far above that of females, and the difference became significant ($P < 0.01$, Analysis of variance, Table V).

Table VI shows that the frequency of behaviour

patterns increased at higher temperatures, and also indicates this increase was not equally proportional among all movements. This general increase in frequency of movements can be seen by inspection of the table. To show the significance of irregularities in the increase, a Chi-square test was performed. Statistical analysis of the data was hindered by the low frequencies of movements observed at 7°C, and behaviour patterns were grouped in an attempt to overcome this problem (see previous section on statistical analysis). The shortcoming was not remedied completely, and results of the analysis must be interpreted with caution. Probably a valid conclusion is: frequencies of behaviour patterns change disproportionately with changes in temperature, but the proportions from figures shown in Table VI may be modified by further data.

DIURNAL EFFECTS.

To reduce locomotor activity measurements, which varied at different temperatures, to a comparable scale, the average activity at four times of day was calculated for each sex and temperature group, and expressed as a percentage, using the average of all distance travelled measurements of that temperature

TABLE VI

Chi-square analysis of change in behaviour with temperature

Holding Temperature	5°C		18°C		
Observation Temperature	7°C	11°C	10°	19°C	Total
Claw-wave and Snatching Movements	3	17	10	35	65
Feeding and Washing Movements	1	21	4	4	30
Digging movements	19	26	53	65	163
Total	23	64	67	104	258

Chi-square 49.9

Degrees of freedom 6

P < 0.001

and sex group as 100%. The resulting daily fluctuations in per cent activity levels are shown in Figure 6.

Locomotor activity of three of the four temperature groups of males was highest at 0530 hours. The fourth group, which was held at 18° and observed at 19°C, showed no change in level of activity in the early morning. Likewise, none of the temperature groups of females showed a peak activity period. The rise in activity, where it occurred, was sufficiently great that it was unlikely to have

arisen accidentally. On the other hand, failure to demonstrate peak activity periods could easily have occurred by chance, because sample sizes were small (each point in Figure 6 is the average of six observations on a total of three crabs). The early morning rise in activity of crabs of some temperature groups was sufficient to suggest later experiments on feeding behaviour should be performed between the hours of midnight and 0400 in order to obtain behaviour recordings at times of greatest activity.

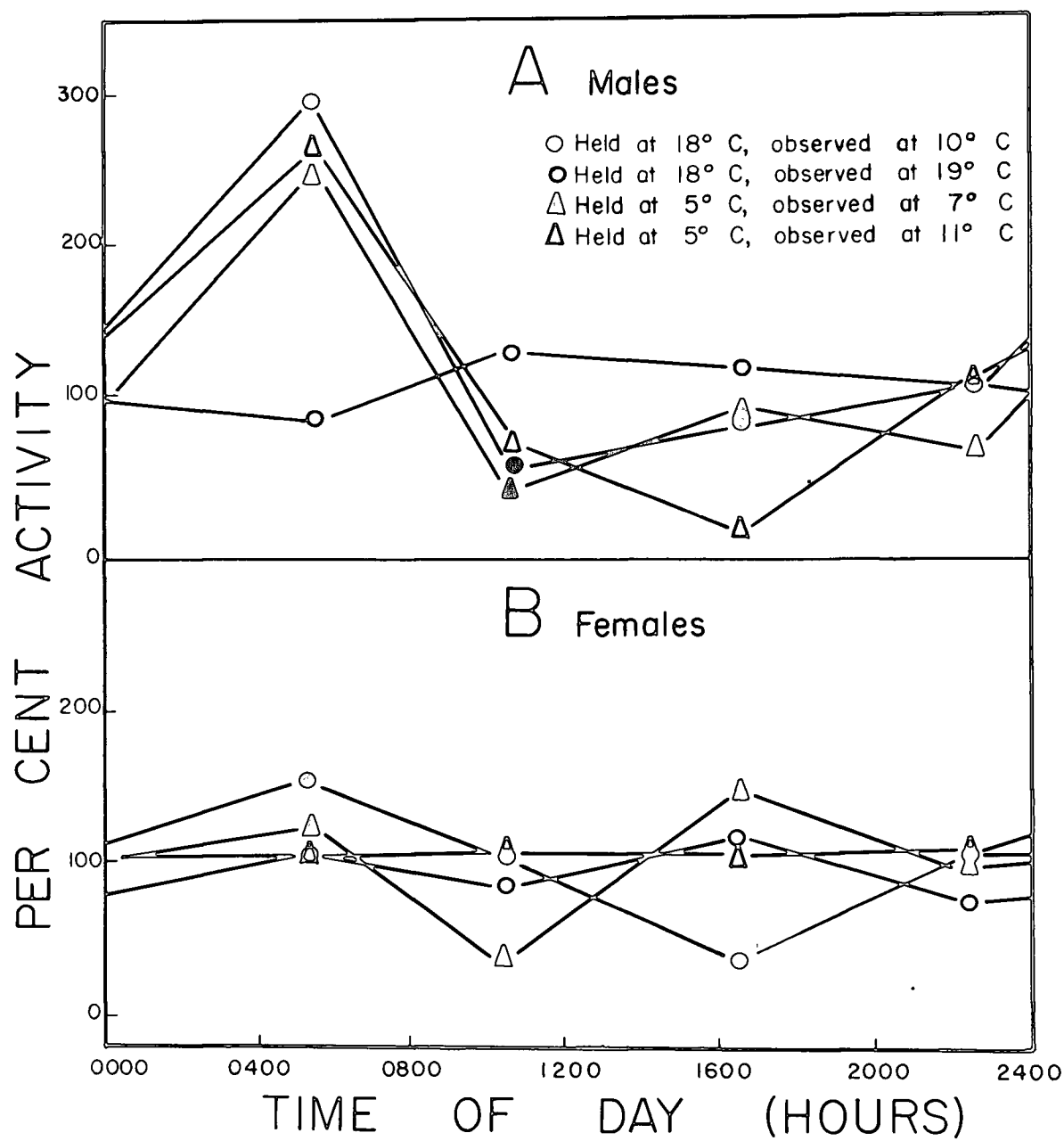
Most behaviour patterns were not sufficiently frequent to permit analysis for diurnal variation, but digging was an exception. Digging showed a tendency to be more frequent during the day, but the increase was not significant ($P > 0.05$, t-test).

SEX DIFFERENCES

Behaviour differences between the sexes of H. oregonensis are apparent in Figures 5 and 6. In three of the four temperatures conditions shown in Figure 5, males were on the average more active than females, though the difference only became significant at the highest temperature conditions ($P < 0.01$, Analysis of variance, Table V). Males showed a rise in locomotor activity in the early morning which was not evident for

Figure 6

Distance travelled, measured as per cent activity in the four temperature groups, plotted as a function of time of day. Each point is the average of six observation on three crabs. The results for males are shown in A, females in B.



females (Fig. 6).

An important difference between the sexes was the increase in variability of activity of females at 19°C observation temperature. If variability was measured by the standard deviation of activity measurements from each observation, variation in activity of females increased from 18.8 inches at 10°C observation temperature, to 74.1 inches at 19°C. Corresponding figures for male crabs were 15.5 inches at 10°C and only 43.7 inches at 19°C. Variability in activity of females at 19°C was almost twice that of males at the same temperature. This variability was of great importance when selecting a suitable temperature for later work on feeding behaviour, and was the major reason for selecting a temperature below 20°C.

Restriction of some behaviour patterns to male crabs was mentioned in the section describing movements. Snatching and creaking movements apparently are restricted to male crabs. Abdomen flapping movements are more common among females.

FEEDING BEHAVIOUR

Only probing and feeding movements were affected by all types of food stimuli, and the changes that occurred are shown in Table VII. In the Time Control

experiments, each movement has been indicated as a response by subtracting numbers of bouts recorded in control periods from numbers of bouts in stimulus periods. In Choice experiments, a response has been indicated by subtracting numbers of bouts occurring on the side of the container furthest from the stimulus, from numbers on the side nearest the stimulus. Where stimuli caused changes in frequencies of other movements, the change has been noted in the text.

Locomotor activity changed upon the introduction of some types of stimuli, and figures indicating the degree of change in Time Control experiments are also given in Table VII. Locomotor activity was not recorded in Choice experiments.

Responses to Food Stimuli.

Chemical Stimuli: Upon the introduction of a liver solution to the observation aquarium, crabs appeared to become excited, and move rapidly about the aquarium making feeding and probing movements. The increases in feeding bouts and in locomotor activity are shown in Table VII, Time Control experiment 1. The number of observations showing an increase in feeding was significant ($P < 0.5$, Binomial test). A similar significance level was obtained from numbers of observations showing an increase in activity. Probing movements were not recorded in this experiment.

TABLE VII

Change in frequency of feeding and probing, and change in motility after introduction of stimuli. Figures were calculated by subtracting numbers of movements and inches travelled in control periods or on empty side of the container, from numbers occurring during stimulus periods or on stimulus side of container.

Type of Experiment	No.	Stimulus Combination	Feeding	Probing	Distance Travelled (inches)
TIME CONTROL EXPERIMENTS	1	Chemical	13*	not recorded	765*
	2	Tactile	10	0	144
	3	Visual & Tactile	17*	0	86
	4	Chemical & Tactile	54*	3	686
	5	Visual, Chem. Chem. & Tactile	37*	10*	499*
CHOICE EXPERIMENTS	1	Visual	2	0	--
	2	Visual	1	0	--
	3	Chemical	16*	17*	--
	4	Visual Choice Chem. excitatory	1	2	--

* numbers of increases are significant,
 $P < 0.5$, nonparametric binomial test
 for small samples.

Other changes in behaviour accompanying the introduction of chemical stimuli included increases in frequencies of climbing, claw-waving and snatching movements. These behaviour changes probably were caused only indirectly by chemical stimuli, and were more directly a result of increased activity. Data gathered during experiments on temperature and diurnal effects, but not presented, have shown that climbing correlates well with distance travelled (coefficient of correlation equal to 0.84). Claw-waving and snatching movements appear to be elicited visually when two crabs approach one another. Since the number of approaches occurring randomly must be higher between active than between inactive animals, the numbers of claw-waving and snatching movements also should be higher. These behaviour changes, therefore, are considered secondary effects of chemical food stimuli.

Release of feeding behaviour by chemical stimuli was shown in Time Control experiment 1. Results of a choice experiment showed chemical stimuli may also direct feeding behaviour. When water that had been in contact with minced beef liver was allowed to diffuse through a porous but opaque plastic screen, forming a gradient of chemical stimuli across the chamber containing the crabs, a greater number of feeding and probing bouts occurred on the side of the compartment nearest

the source of the stimulus. The difference in frequency of bouts is shown in Table VII, Choice experiment 3. The number of observations showing an increase was significant ($P < 0.05$, Binomial test).

Tactile Stimuli: Blinded crabs reacted to small pieces of gum eraser by picking them up and attempting to feed on them. This response occurred as soon as a crab walked onto a piece of eraser. The resulting increase in numbers of feeding bouts is shown in Table VII (Time Control experiment 2). The number of observations in which an increase occurred was not statistically significant (Binomial test), but evidence supporting the response indicated, was afforded by the experiment with combined visual and tactile stimuli (Time Control experiment 3, Table VII). The response in the combined stimuli experiment probably was due exclusively to tactile stimuli, as visual stimuli have not been shown to affect feeding behaviour. Later experiments on starvation also supported the conclusion that pieces of gum eraser released feeding movements.

If the assumption is accepted that crabs respond to tactile qualities of gum eraser that resemble their natural food, the conclusion can be stated that feeding movements are released by tactile food stimuli. This type of stimulus does not, however, cause an increase either in probing movements or in locomotor activity.

Visual Stimuli: The directing effect of visual food stimuli was measured by placing minced beef liver (Choice experiment 1) or a live sculpin (Choice experiment 2) in one end of a tripartite box, and recording the behaviour of two crabs in the center compartment. No statistically significant differences (Binomial tests) were shown when numbers of observations showing positive responses were compared with numbers showing negative responses. Figures in Table VII show crabs are not directed by sight of liver or of sculpins, but no measure of releasing components of visual stimuli is given.

A measure of the releasing ability was obtained by comparing the frequency of feeding bouts in the control periods of Time Control experiments with the frequency of feeding bouts recorded during visual choice experiments. In all control periods, when food was absent, the frequency of feeding bouts was 1:20 bouts per crab per hour. When food was visible, frequency of feeding was 0.80 and 0.20 bouts per crab per hour with liver and sculpins respectively. The frequency of feeding bouts when food was visible, was actually lower than when it was absent. Therefore neither of the two types of visual stimuli, when presented alone, either direct or release feeding behaviour.

The possibility remained that visual stimuli

direct the animal once feeding behaviour has been released by some other stimulus. To test this possibility, crabs were excited with liver extract used as a chemical stimulus, and simultaneously confronted with a choice situation using minced liver as the visual stimulus. Though frequency of feeding was raised to 3.40 bouts per crab per hour, numbers occurring at each side of the container were nearly equal (Choice experiment 4, Table VII). Results for probing movements were similar. Once again, visual stimuli apparently were ineffective.

Effects of combining Stimuli: Visual stimuli in combination with tactile and chemical stimuli did not appear to have a consistent or a large effect on behavioural response. A small increase in feeding response occurred with the addition of vision to tactile stimuli (compare feeding in Time Control experiments 2 and 3, Table VII). However, a slight decrease in feeding occurred when vision was added to combined chemical and tactile stimuli (compare feeding in Time Control experiments 4 and 5, Table VII). Probing caused by combined chemical and tactile stimuli increased slightly upon the addition of vision to the combination (Time Control experiments 4 and 5). These effects, and especially effects on locomotor activity (see below), may have been caused by blinding which was necessary

where vision was to be excluded. Effects of blinding are described later.

The highest frequencies of feeding response were elicited by combined chemical and tactile stimuli. Later experiments on starvation, in which observations using separate and combined stimuli were repeated at different starvation levels, supported this (Fig. 8B).

Probing and increased travelling responses, in contrast to feeding, were not released at consistently highest frequencies by combined stimuli. Probing responses to chemical stimuli in later experiments on starvation exceeded the response to combined chemical and tactile stimuli (Fig. 8A). Similarly, increased locomotor activity response to isolated chemical stimuli (Time Control experiment 1, Table VII). However, an inconsistency in this response occurred at the 5 day starvation period shown in Figure 8 C, where response to combined stimuli exceeded the response to isolated chemical stimuli.

Effects of Blinding.

An experiment comparable with presentation of chemical stimuli to normal crabs was conducted using blinded crabs. The purpose was to compare feeding responses of blinded animals with normal, when both received the same food stimuli. Result from this experiment showed such abnormally high frequencies of feeding

that the experiment was repeated, and on repetition, a much lower value was obtained. However, data from the two runs were significantly different ($P < 0.05$, t-test), and therefore averaging these data could not be justified. Rather than presenting unreliable and possibly misleading figures, results of the experiment have been omitted, and conclusions concerning the effects of blinding have been drawn from results of other experiments with blinded crabs (Time Control experiments 2 and 4, Table VII).

Performance of claw-waving and snatching movements, both apparently elicited by vision, were not prohibited by blinding, though their frequencies may have been reduced. Probably these behaviour patterns can be released by tactile stimuli as well as by vision.

Locomotor activity of blinded crabs was approximately three times that of normal animals. This increased activity was the most noticeable effect of blinding, but whether it was caused by irritation of the eye stalk by the plastic aluminum coating, or whether it resulted from the sensation of darkness presumably experienced by blinded crabs, is not known. Lack of special equipment needed for investigation of these possibilities prohibited further work.

Comparison of feeding behaviour in experiments where vision was absent with experiments where

visual stimulation was permitted, showed there were no great differences between the two conditions. Two conclusions are indicated: (1) sight of food does not influence feeding behaviour and (2) blinding does not unduly influence feeding behaviour. Though both vision and blinding may affect other aspects of behaviour, these two conclusions were considered ample justification for use of normal animals in later experiments on starvation effects of responses to chemical and tactile stimuli.

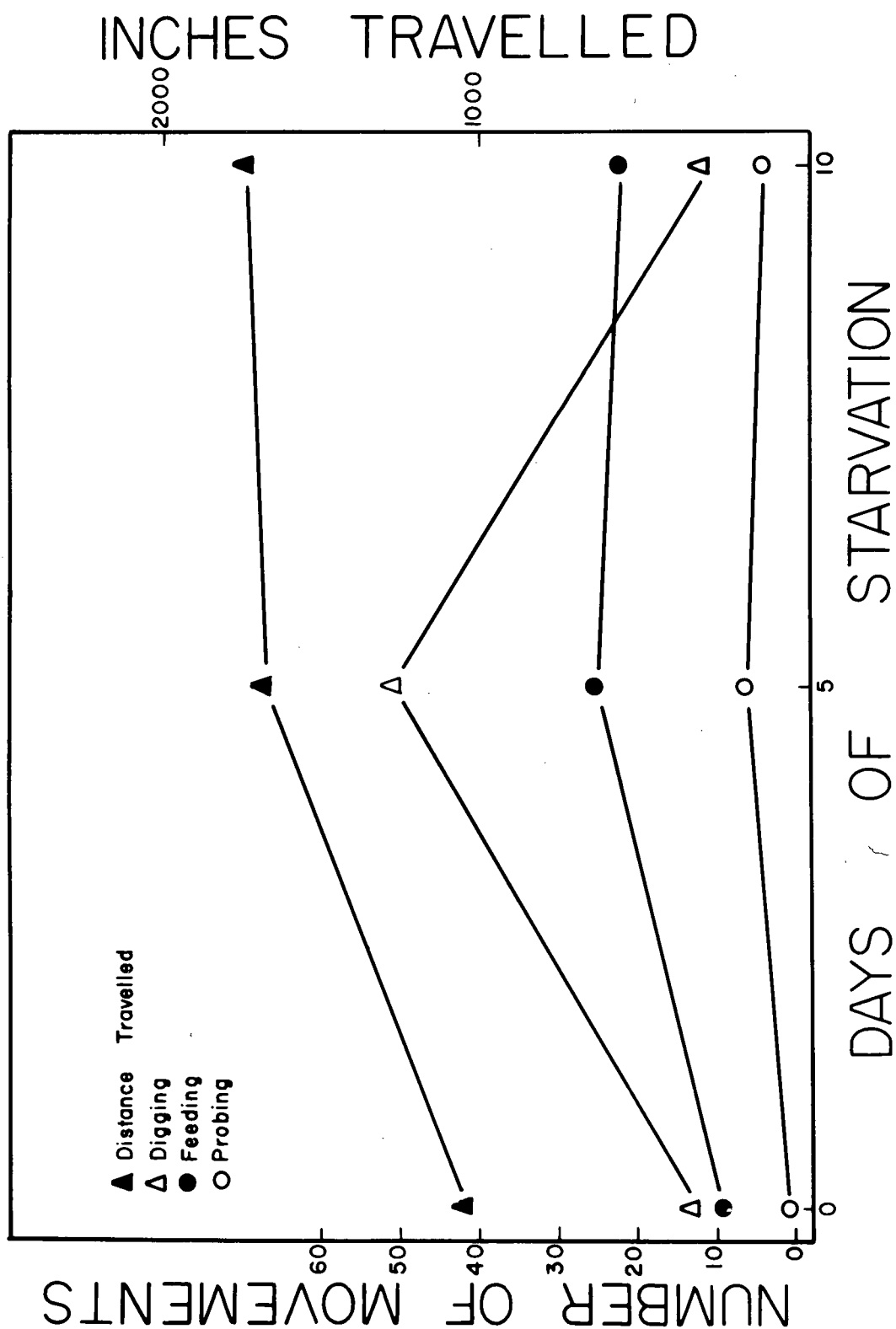
Effects of Starvation

The effects of starvation were measured by presenting tactile and chemical and combined chemical and tactile food stimuli to crabs at the end of five and ten days starvation. Pieces of gum eraser simulating tactile stimuli, and liver extract as chemical stimuli, were presented in the same manner as before. This procedure permitted comparison of previous results with results from starved animals. Normal (unblinded) crabs were used throughout.

The general effects of starvation are depicted in Figure 7, where frequencies of four behaviour patterns are shown. These are the changes which occurred in the absence of food stimuli. They have been obtained by summing the number of bouts and number of inches occurring in control periods alone, at each level of

Figure 7

Showing changes in behaviour at three levels of starvation when no food stimuli were present. Only probing, feeding and digging movements showed a change.



inches occurring in control periods alone, at each level of starvation. Digging movements increased markedly after five days, then dropped to near the original level after ten days starvation. Though this change was significant ($P < 0.05$, t-test), its cause was unknown. Figure 7 shows that probing increased from a total of zero to six bouts and decreased to four bouts at zero, five and ten days starvation respectively. Distance travelled, however, showed a steady increase from a total of 1639 inches at zero days starvation to 1667 inches at five days to 1743 inches at ten days starvation.

To demonstrate change in responses, these general behaviour changes were taken into account by the method of calculation employed (subtraction of figures in control periods from stimulus periods). Therefore the changes in responses shown to be caused by starvation are modifications occurring in addition to the general behaviour changes. Digging was not considered a feeding response and has been omitted from further discussion. Effects of starvation on probing, feeding and activity responses are shown in Figure 8.

Probing Responses

To Chemical Stimuli: Unfortunately probing was not recorded at zero days starvation, but a slight increase in response to the liver solution between five

and ten days starvation is evident in Figure 8 A.

To Tactile Stimuli: Probing was not elicited from recently fed crabs by tactile stimuli, but after five days starvation, a response occurred. Levels of response at five and ten days starvation were approximately similar.

To Combined Chemical and Tactile Stimuli: The number of probing bouts released by combined stimuli was about half the number released by chemical stimuli. Change in response with progressive starvation was not constant, but the highest response occurred after ten days starvation.

Feeding Responses -

To Chemical Stimuli: Feeding response to liver extract increased rapidly and consistently with starvation (Fig. 8B).

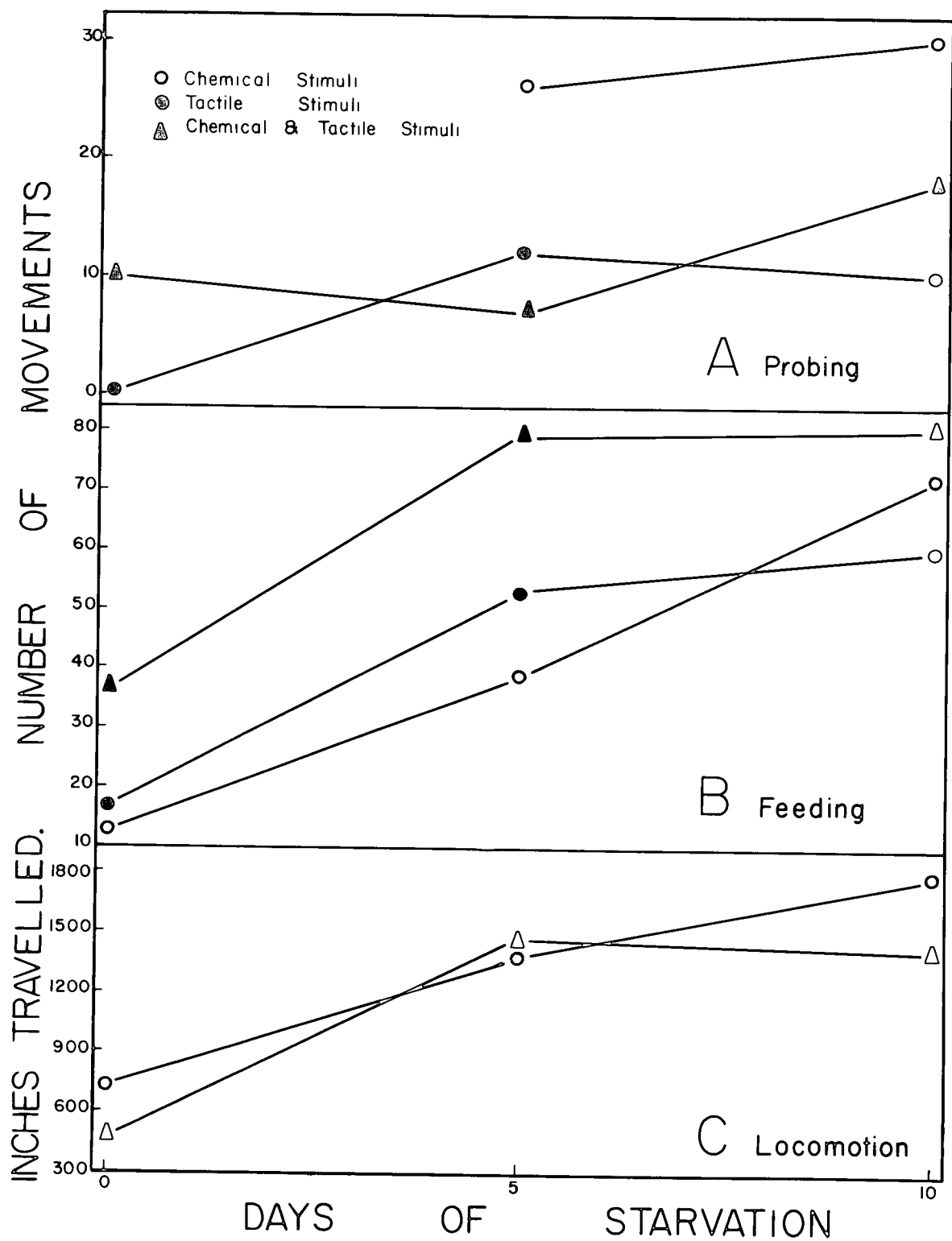
To Tactile Stimuli: Response to pieces of gum eraser increased most after the first five days of starvation, and showed a smaller increment between five and ten days starvation.

To Combined Chemical and Tactile Stimuli: At all levels of starvation, feeding response to combined stimuli was greater than to separate stimuli. Feeding response to combined stimuli changed with starvation in a manner similar to starvation changes of feeding responses to tactile stimuli.

Figure 8

Effects of starvation on responses to chemical, tactile and combined chemical and tactile stimuli.

- A. Changes in probing response,
- B. Changes in feeding response, and
- C. Changes in motility response.



Locomotor Responses -

To Chemical Stimuli: Locomotor activity in response to chemical stimuli showed a consistent increase with progressive starvation (Fig. 8C). Distance travelled increased approximately 600 inches upon each five day interval of starvation.

To Tactile Stimuli: There was no significant (Binomial test) locomotor response to tactile stimuli at any level of starvation.

To Combined Chemical and Tactile Stimuli: Locomotor response to combined stimuli increased after the first five days starvation, but changed little in the succeeding five days. Response to simultaneous stimulation tended to be lower than to chemical stimuli except at five days starvation, where the response was slightly greater (Fig. 8C).

DISCUSSION

A change in the environment is almost always accompanied by changes in behaviour, and for the most part the behavioural changes assist in returning the animal to a state of equilibrium with the environment. The behaviour of Hemigrapsus oregonensis has been described when the crab was subjected to several environmental conditions which included variation in tempera-

ture and diurnal light intensity, and presentation of different food stimuli after varying periods of starvation. These are environmental changes which easily could, and often do occur in field conditions, and the behaviour of the crab must be adapted to them.

Temperature and behaviour:

The effect of temperature on activity of poikilotherms is well known (Bullock, 1955; Prosser, 1955), and results of the experiments on H. oregonensis agree with the generalization that activity of poikilotherms is raised by high temperatures and lowered by low temperatures, providing these temperatures do not approach the lethal limit. This dependence of activity on the environmental temperature is a disadvantage for which some poikilotherms partly compensate by "acclimation". An animal able in some degree to acclimate, shows a compensatory change when held over a period of time at habitat or environmental temperatures. The animal's activity, raised or lowered by the high or low acclimating temperature, tends to return towards the normal level. Acclimation can be demonstrated by holding animals at the extreme temperatures and measuring and comparing their activity rates when returned to an intermediate condition. If compensation has occurred, the rates of animals from high temperatures will be lower, and rates of animals from low temperatures will

be higher than the rate of animals held and measured at the intermediate temperature.

Locomotor activity measurements on H. oregonensis which have been held eight days at temperatures of 5° and 18°C, show that a change has taken place when measurements were made at intermediate temperatures of 11° and 10° respectively. Animals held at the high temperature were more active at the intermediate temperature than animals held at the low temperature (Fig.5). This indicates the locomotor activity of animals from one or both holding temperatures have failed to return to the level normally occurring at the intermediate temperature. Data are not sufficient to describe the changes in detail, but only partial compensation may have occurred.

Behaviour of rates of locomotor activity and oxygen consumption of H. oregonensis differ when their reactions to temperature acclimation are compared. Oxygen consumption of summer crabs (H. oregonensis) in 75% sea water from two acclimation temperatures 5° and 20°C demonstrate compensation by a lowering of the rate in crabs from high temperatures and a raising of the rate in animals from low temperatures when both are measured at 10°C (Dehnel, 1960). This is not the case with rates of locomotor activity. Data from crabs held and measured at intermediate temperatures were not ob-

tained, and therefore conclusions concerning changes in motility are restricted. However, compensation has not proceeded to the point demonstrated for oxygen consumption because motility rates of crabs from the high acclimation temperature remain higher than rates of motility in crabs from the lower holding temperatures when both are measured at approximately 10°C.

Fry (1947) has noted that two rate functions may behave differently. This difference could have considerable biological significance for, if oxygen consumption and locomotor activity measure two different physiological processes which possess unequal rates of equilibration to temperature change, rapid temperature changes will force the two rate functions out of phase. Slow temperature changes would allow constant readjustment of the two processes, the crab would be in a state nearer to homeostasis, and as a result could probably tolerate more extreme temperature changes. Todd and Dehnell (1960) show that acclimation for twenty-four hours (which allows time for readjustment of processes) to 20°C in 75% sea water increases the higher temperature tolerance of summer animals 1.22°C over values tolerated by animals with no laboratory acclimation. They suggest that a rapid gain in tolerance over a period of a few hours would be most advantageous to this crab as some tide pools in the Spanish Bank area have been recorded

at temperatures as high as 26° to 28.5°C.

The frequency of all behaviour patterns investigated increases at higher temperatures (Table VI). Some evidence is presented suggesting the increase in frequency is not equal between different movements, but more data supporting and clarifying these disproportionate increases are needed before their adaptive value can be assessed.

Diurnal Rhythms of Behaviour:

Diurnal chromatophore rhythms in the crab Uca (Brown and Webb, 1949), and activity rhythms in the cockroach Blatta orientalis (Gunn, 1940), have been shown to continue for several days in the absence of any known environmental stimulus, and for this reason centers of rhythmicity have been postulated as a control of these daily changes in behaviour. Experiments on Hemigrapsus oregonensis demonstrate a diurnal rhythm of locomotor activity, but, as light intensity varied between night and day, data cannot be used to show a spontaneous rhythm. However, the change in locomotor activity of male crabs at times when light intensities were equal (2230 hours and 0530 hours), suggests the rise in activity at 0530 hours (Fig. 6A) was dependent on some factor other than low illumination. Possibly chromatophore rhythms and activity rhythms have a common physiological controlling mechanism.

The adaptive significance of this early morning rise in activity is apparent, for avoidance of the hot dessicating sun during the summer months is advantageous. Both H. oregonensis and Pachygrapsus crassipes which also is nocturnal (Hiatt, 1948) can live for hours, possibly even for an indefinite period, out of the water so long as their gills remain moist.

The inconsistency of results (see Figure 6) might have been clarified by use of brighter illumination than 20 foot candles. This is suggested by the results of Brown and Webb (1949), who found the chromatophore rhythm of Uca was reversed faster when brighter illumination was supplied. Illumination of 150 foot candles reversed the rhythm in one day, 80 foot candles in three days, and with 40 foot candles reversal occurred on the fourth day.

Behavioural Differences between Sexes:

Differences in behaviour between the sexes are probably directly or indirectly a result of the particular role played by each sex in reproduction. Higher activity of males in three of the four temperature conditions shown in Figure 5, suggests that males perhaps take the active role in finding a mate as well as taking the initiative in copulation. Greater variability in activity of females than of males was shown at 19°C, but possible advantages of this behaviour are

obscure.

Differences in reproductive behaviour of the sexes include restriction to males of such movements as creaking and snatching. Both these behaviour patterns appear to function in pairing male crabs with female. Selection of a possible mate by a male crab initially is random. The male seeking a mate may rush at the selected animal catching it with a snatching movement of the claws. Copulation attempts between two males apparently are inhibited at this point by the performance of creaking by the caught male. This method of pairing is relatively unspecialized compared to the elaborate courtship displays of some animals, but is not poorly adapted to survival of the crab. Males and females at the beach are present in almost equal numbers (personal observation) so that random selection of a mate brings approximately 50% success, and performance of the creaking movement evidently prevents ill consequences resulting from copulation attempts between two males. Crayfish do not appear to have evolved an inhibitory motion such as creaking, and males may suffer considerable damage in attempts to copulate with one another (Scott, 1958).

Feeding Behaviour:

To most animals, a major obstacle to survival must be the sorting of sensory messages so that appro-

priate behaviour occurs in any given environmental situation. Shore crabs are confronted with a series of objects varying from orange peel to dead animal to algae, all of which might be suitable food. Three behavioural mechanisms might be suggested for release of appropriate responses to various stimuli. The animal may learn the import of each stimulus encountered, or may possess an inherited releasing mechanism for particular stimuli. Both these mechanisms would appear to require complex nervous systems when operating with a wide variety of stimuli. The third mechanism is actually a variation of the second; the animal instead of possessing an innate releasing mechanism for one or two particular stimuli, reacts to a property possessed in common by all the stimulus objects. This last appears to be the mechanism adopted by H. oregonensis for releasing feeding responses at appropriate times. Feeding behaviour can be elicited by a soft object, pieces of gum eraser suffice, and probably by some general chemical quality of meat. Learning, however cannot at present be eliminated as a possible explanation for reaction to these general stimuli, even though the learning ability of crabs is probably not great (see Yerkes, 1902).

Conclusions concerning the results on visual food stimuli must be made with caution. A negative result, such as the lack of response shown, is almost im-

possible to prove and may be caused by a variety of factors such as strangeness of the experimental situation and use of inadequate or incorrect stimulus objects. Hiatt(1948) was able to show a positive response to sight of food with the crab Pachygrapsus crassipes by dropping pieces of food near the animal. After a moment of hesitation the crab would approach the object. When the crab was submerged in water, the response was sufficiently immediate that Hiatt claimed chemical stimuli could not have had time to reach the animal. In air, Hiatt could show no response to chemical stimuli, and therefore response to food dropped near a crab must have been due to vision.

However, the previous considerations concerning the use of generalized stimuli for release of feeding behaviour, supply a good reason for the hypothesis that feeding behaviour of H. oregonensis is not released by visual stimuli. No distinguishing visual property is possessed in common by a worm, green alga, and a dead sea gull. Yet this crab probably eats all of these. Clearly, vision might be more adapted as a receptor system warning the crab of an approaching predator, since most predators have in common the visual properties of a large object moving rapidly. Certainly crabs can be observed scuttling for the nearest cover whenever a person walks along the beach, regardless of the quiet-

ness with which the person may move his feet.

Chemical stimuli are effective at a distance from their source, and, reasonably, they direct and stimulate appetitive searching behaviour in the form of probing movements and locomotion (Table VII). An observer making a subjective appraisal of the behaviour would say the crabs become excited upon the presentation of chemical stimuli. The animals make short dashes in various directions all the while probing with their claws into the sand as if searching for food. Tactile stimuli are effective only when the crab is in direct contact with food. Correspondingly, tactile stimuli release the consummatory act of feeding; appetitive behaviour is not stimulated. Chemical stimuli are as effective at close range as at a distance, and they too release consummatory feeding movements. The whole sequence of feeding behaviour from appetitive behaviour patterns up to the consummatory act of feeding itself (nothing is known of swallowing movements) can be released by chemical stimuli alone. No food is necessary.

Release of the entire sequence of behaviour patterns by a part of the whole stimulus in feeding behaviour of H. oregonensis contrasts with reproductive behaviour of many other species of animals. Tinbergen (1951, 1953) has stressed the necessity for the complete sequence of sign stimuli to release egg laying in

the three spined stickleback, Gasterosteus aculeatus. Among invertebrates, males of the spider Pardosa milvina court only when stimulated by correct tactile and chemical stimuli simultaneously. Both stimuli are necessary, no courting response is elicited by either stimulus alone (Savory, 1959). The need for two or more different stimuli to be presented simultaneously in order to obtain a response, has been termed heterogenous summation. The tendency to restrict responses to times of concurrent stimulation ensures the release of particular behaviour patterns only in appropriate situations. Such specificity in timing of responses is unnecessary in feeding behaviour, and consequently one type of stimulus is sufficient to release a response.

However, though not all parts of the total food stimulus are necessary to release feeding behaviour, changes in response do occur when both chemical and tactile stimuli are presented simultaneously. This change is quantitative; the number of feeding movements is nearly doubled by presenting both stimuli together (Fig. 5B). Nerve impulses from chemoreceptors and tactile receptors presumably have summed to increase the frequency of feeding response. Though probably of common occurrence, summation which alters the degree of response has seldom been described. The most complete previous account was given by Seitz (1940), who worked

with the fish Astatotilapia strigigena.

Chemical and tactile stimuli when combined increase the frequency of the consummatory act of feeding (Fig. 5B), but do not increase the appetitive responses of probing and locomotion (Fig. 5A and C). The amount of probing at zero, five and ten days starvation, and locomotion at zero and ten days starvation, is decreased from the level elicited by chemical stimuli alone when tactile stimuli are added (Figs. 5A and C). As a crab approaches a piece of food, more and more of the component food stimuli are received. These stimuli apparently summate to increase the consummatory response, and ultimately, upon the reception of all component food stimuli, appetitive behaviour patterns presumably would cease, giving way almost entirely to consummatory feeding behaviour.

Effects of Starvation on Behaviour:

Starvation causes marked changes in behaviour. Changes found from these experiments included increase in the three feeding responses: feeding movements, probing movements and distance travelled. Starvation increased these both in the presence and absence of food stimuli (Figs. 4 and 5). Digging movements increased after five days starvation, but then decreased to near the original level upon ten days starvation (Fig. 4).

With the exception of the change in digging

frequency, which cannot be explained at present, these changes in behaviour aid the animal by directing it to food. The increase in locomotor activity of hungry crabs both in the presence and absence of food stimuli is particularly useful in this context. A rise in the number of probing movements increases the chances of finding food buried in the sand. The increase in the consummatory act of feeding when food stimuli are absent can be understood if one considers that hungry crabs respond to less specific food stimuli than satiated animals. By attempting to eat objects that normally do not excite feeding behaviour, starved crabs may pick up food that otherwise would be overlooked. The behavioural mechanism adapting the animal to a food shortage appears to be a lowering of the threshold of feeding responses to food stimuli.

Extension of the idea that starvation lowers the threshold so that normally unacceptable objects acquire the ability to stimulate feeding, leads to the hypothesis that feeding movements may occur without any external stimulation. Behaviour occurring spontaneously in the absence of appropriate stimuli, has been termed vacuum activity (Leerlaufreaktionen, in Thorpe 1956) or overflow activity (Armstrong, 1950, in Thorpe, op.cit.). As an explanation for the increased frequency of feeding movements in control periods where no food stimulus

was supplied, the concept of vacuum activity has two objections. First, sand grains and small stones may have been acting as food stimuli. Proof of the absence of appropriate stimuli is difficult, if not impossible, even under the most favorable circumstances. Second, the adaptive value of vacuum activity to the animal is uncertain. Behaviour occurring with no appropriate stimuli, and therefore to no apparent purpose, has doubtful use as an aid to survival. The argument that performance of vacuum activity consumes specific action potential relieving the animal from an accumulation of nervous tension which is somehow detrimental, is a rationalization too hypothetical to be satisfactory. The hypothesis of "lowered threshold" provides a suitable explanation for feeding movements occurring in the control period, and avoids the two objections raised by the concept of vacuum activity.

As starvation proceeded, the number of feeding movements released by separate tactile and chemical stimuli drew nearer the number released by combined chemical and tactile stimuli (Fig. 5B). When the threshold of response is lowered by hunger, parts of the total stimulus become nearly as effective as the whole in their ability to release consummatory feeding behaviour. Sensitivity to food is increased.

Behavioural Mechanisms:

In the course of discussing changes in behaviour adapting the animal to a changed environment, several behavioural mechanisms have been postulated. These mechanisms have included phenomena controlling releasing and directing components of feeding responses, heterogenous summation of stimuli, and lowering of the threshold of response to stimuli. Whether these behavioural mechanisms have each a discreet physiological counterpart, or whether they are the result of more general neural processes is unknown. One of the first steps in answering this question will be the location of the areas in the nervous system from which the change in behaviour is controlled. For instance, in vertebrates, change in need appears to affect behaviour through changes in the central nervous system rather than through changes in sensitivity of the receptor organ. Experiments on rats (Pfaffman, 1957) suggest that the taste receptor organs are unaffected by a need for salt. Electrodes attached to the chorda tympani nerve of rats showed that nerve impulses were the same in normal and adrenalectomized, and therefore salt deficient animals. Pfaffman states, "It is concluded that changes in behaviour under these conditions reflect not a change in the peripheral afferent neural message, but in its significance for central neural processes".

Location of neural mechanisms governing behaviour changes within the central nervous system of vertebrates, is no reason to assume that similar behavioural changes in invertebrates also will be controlled from the central nervous system. The process of myoneural inhibition, for instance, occurs within the central nervous system of vertebrates, but at peripheral junctions in crustacea (Hoyle, 1957). In vertebrates, the regulation of food intake appears to be controlled in part by areas of the hypothalamus (Anliker and Mayer, 1957), but the peripheral receptor organs also apparently play a part in this control (Quigley, 1955). Centers controlling behavioural changes resulting from starvation in Hemigrapsus oregonensis may or may not be located in the central nervous system. The decision must await further work.

SUMMARY

1. Basic behaviour patterns of Hemigrapsus oregonensis were described. Some of the most frequently occurring movements were: "standing", "walking", "feeding", "claw-waving", "digging", and some motions apparently belonging to reproductive behaviour including, "snatching", "creaking", and copulation. Behaviour was quantified in further experiments by recording the numbers of bouts of these movements per observation period.

2. Behaviour and locomotor activity varied with temperature. Crabs from two holding temperatures (eight days at 5° and 18°C), were observed at temperatures approximating their own holding condition (crabs held at 5° were observed at 7°C; those from 18° were observed at 19°C) and also at an intermediate condition (temperatures of 10° and 11° C). Results showed activity and frequency of behaviour patterns were greatest at the highest temperature. However, the frequencies of behaviour patterns appeared to increase disproportionately from low to high temperatures, and the past thermal history of the crab affected activity so that animals from the higher holding temperature were more active than those from the lower, when both were observed at the intermediate condition.

3. Locomotor activity measured at 0530, 1030,

1630 and 2230 hours of the day, showed a peak activity period in some temperature groups of male crabs at 0530 hours. This activity period may have resulted from the reduced light intensity used for night observations.

4. Comparison of behaviour between sexes showed males tended to have a higher rate of locomotor activity, but that variability in this activity was greatest among females at high temperatures (19°C), being double that of males at the same condition. Performance of the reproductive behaviour patterns of snatching and creaking were apparently restricted to male crabs. Creaking appeared to act as an inhibitory movement, preventing one male from attempting copulation with a second male animal.

5. Crabs were tested for response to visual, chemical and tactile food stimuli, and tactile and chemical stimuli were shown to be effective. Behavioural responses to a solution of minced beef liver (chemical stimuli) consisted of an increase in frequency of probing and feeding behaviour patterns and an increase in locomotor activity. These responses were both directed and released by the chemical stimulus. Blinded crabs responded to the tactile stimulus of gum eraser by showing an increase in frequency of feeding bouts. No response could be demonstrated to sight of minced

liver or sculpins, and the effects of vision in combination with chemical and tactile food stimuli appeared negligible. The possibility that crabs react to generalized stimuli possessed in common by different types of food was discussed with reference to these findings.

6. Presentation of combined chemical and tactile food stimuli caused a greater increase in frequency of feeding bouts than presentation of only one type of stimulus at a time. An increase in degree of response by addition of various types of stimuli to the environment is an example of heterogenous summation. No summation occurred in appetitive behaviour responses of probing and increased activity.

7. Starvation for five and ten days increased the degree of all responses to both chemical and tactile food stimuli, though only feeding showed consistently highest frequencies at the ten day starvation level. Probing and locomotor activity in response to some stimulus conditions were highest at five day level. The experiments showed that starvation apparently lowers the threshold level of response to food stimuli.

8. While the behaviour of H. oregonensis is not complex in comparison to that of other animals, consideration of its reproductive behaviour and response to generalized types of food stimuli, and also of

the behavioural changes occurring with variation in temperature, time of day and degree of starvation, showed each of these aspects plays a part towards the survival of this crab in its environment. .

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