Sense of Smell and Pair-Bond in *Hymenocera picta* Dana[1]

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Abstract

Hymenocera picta Dana has functional eyes and is able to recognize conspecifics by sight over 20 cm away. Prey, however, is identified by smell and located by the shrimp moving upstream as long as the scent is perceived. Scents are perceived by the waving antennules which have a single row of sensory hairs on their terminal lobes. *Hymenocera* are normally found in pairs: 93.5 per cent heterosexual and 6.5 per cent homosexual. Therefore, both sexes must be able to identify the sex of a conspecific. Using only scent-cues, the shrimp does prefer conspecifics over other crustacea. Males identify by scent only and prefer their own female over any other conspecific. A pheromone is produced only by the female and perceived by males only. Motivation analysis shows that the pair-bond (the attachment to a particular individual of opposite sex) in *Hymenocera* is not part of the agonistic, or sexual, or brood-care behavior complex, but is based on a special "drive for attachment". We suggest that attachment to a conspecific in *Hymenocera* is a means of reducing stress in the individual.

In a preceding paper, the general biology of *Hymenocera picta* Dana has been described, including the fact that these animals are found in pairs (Wickler, 1973-this issue). Over the period of one year, we put to protocol all the pairings among 65 animals (28 females and 37 males). From a total of 1352 pairings, 95.5 per cent were heterosexual, 3.3 per cent were male-pairings, and 3.2 per cent were female-pairings. Therefore, females as well as males must be able to correctly identify the sex of a conspecific.

We were able to sex these shrimps by special, but inconspicuous color-markings on the abdomen and the pleopods (Wickler and Seibt, 1970). The animals, however, obviously did not rely on these characteristics; young, sexually immature females were externally indistinguishable from males but were nevertheless treated like females by their conspecifics. Further, sex recognition among the shrimps did not fail even in complete darkness. We conclude from this that it is by chemical signals that these animals identify the sex of a conspecific. Since the animals proved able to correctly identify the sex of a conspecific at any time chosen for our experiments, these signals must be given off continuously and from some time prior

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to sexual maturity onward. These suggestions have been tested in a special experimental design described below.

Before copulating, the male shows several intensive behavior patterns directed towards the female (see Wickler and Seibt, 1970 and film E 1725 of the Encyclopaedia Cinematographica). We refer to these activities as "courtship" in a purely descriptive sense without suggesting any special functions to them. This courtship is limited to the time of female moulting. Usually all males in a tank will then be activated and court. This specific activation of males may be used as a biotest for analyzing the signals leading the male to copulation.

A small quantity of water from a tank in which a female has just moulted, poured into another tank containing males, will activate these males to court any available female. We conclude from this that there is a chemical signal released by the moulting female which attracts the males. However, none of our animals, whether male or female, was ever activated by its own moulting. The simplest explanation for this is a sex-specific emission and perception of the signal in question. Since males obviously are able to perceive this signal but do not react to a moulting male, the signal must be emitted by females only. Since this signal, though emitted by females, does not in any way activate females, we have no reason to believe that females are able to perceive this signal.

Observations over long periods showed that in most cases the same individuals stayed together as a pair. However, every individual has a specific area in the tank where it can be found with a high degree of probability. The animals avoided open sand areas and preferred small cavities between stones over dense algal vegetation. Small artificial caves (halves of small flower pots) made an area more attractive. Long term observations at few hour intervals over many months (normally during day time, and only for a limited period continuously over several 24-hour cycles) of the exact position of each individual in a tank with ample caves showed that nearly every individual was located in a specific area of the tank. Thus, they had a clear preference for an area without being confined to it. If there was food outside the preferred area, the animal would go out and try to retrieve it back to the preferred location. Often two animals of opposite sex preferred the same locality. So, pair-stability could be due to the fact that both animals preferred the same locality.

Therefore, we removed the female of an established pair and placed her, confined under a small net, elsewhere in the tank. We did this several times with each female, each time placing her in a different locality. This was done with six females of different pairs. Although in every test there were other females available in the tank, none of the males went to a "wrong" female. All went to their particular female and stayed with her. These tests, in which one member of a pair was experimentally transferred to another place show (1) that there is individual recognition of the female by the male (Seibt and Wickler, 1972), and (2) that the male is attached to a particular female. Attachment here means "seeking and maintaining proximity to another individual" as defined by Bowlby. An attachment between male and female we call "pair-bond".

The males stayed with their particular females which were still confined under the nets. If food was offered at some distance, the male would leave the net, pick up the food, and carry it back to the net with the female. If the female is removed completely from the tank, the male will finally return to its preferred locality. Should the female, however, be somewhere else in the tank and—because of the net—unable to return, the male will carry the food to the female's site. This indicates a pair-bond that is stronger than the territorial bond. Pair stability, thus, is achieved by the attachment of a male towards an individually recognized female. The experiments with the displaced females did not fail even in complete darkness; this suggests that individual recognition, too, is based on chemical cues.

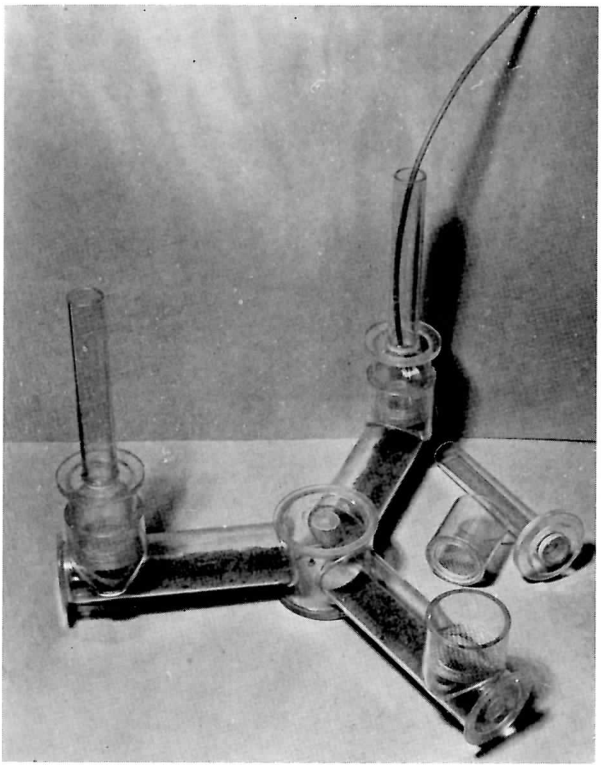

Fig. 1. Y-maze, explanation in text.

This was tested in a Y-maze (Fig. 1). Most of the experiments were done with males because females did not react very well. The test-male was placed in one branch of the maze; above him water was sucked out so that the other two branches acted as inflows. In each of these branches, the water passed over one site. The two currents, loaded with different odors, converged in the center where the male had to make a decision. If he moved into one branch and stayed there for three minutes, this was counted as one choice. The "chimneys" then were exchanged at random and the male had to make another choice, and so on. Control tests were run to rule out side-preferences.

The results of these experiments are as follows. Males and females in 80 tests, run on 17 different days, clearly preferred the current carrying food odor over an "empty" current. Both sexes preferred, similarly, the odor of conspecifics over that of a different species or over "no odor". Males preferred females over males; they did not distinguish between two different males; large and small females or females with or without eggs were treated alike. Again, as in the experiments described earlier, members of a pair preferred their mate over strange individuals.

In these tests, the animals found food by smell only. We know from behavior observations that they are able to recognize conspecifics by sight over 20 cm away. However, they never reacted to food by sight only. If we put a starfish in their tank, they reacted with orientation movements—as shown in film E 1724—by

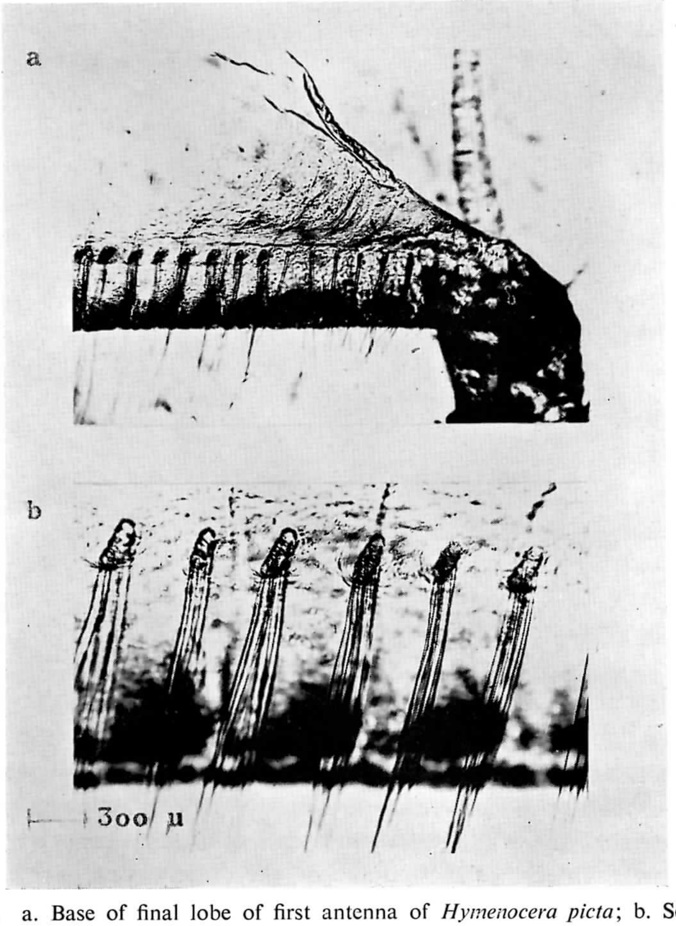

Fig. 2. a. Base of final lobe of first antenna of *Hymenocera picta*; b. Sensory hairs on that lobe (enlarged).

heavily waving the antennules. The shrimps then moved upstream until they came upon the prey or lost the scent; in this case, they started searching, moving randomly about.

The sense of smell is located on the first antennae (Fig. 2a). Their final lobe is broadly expanded and bears one single row of sensory hairs (Fig. 2b). For the effect of monogamy upon the reproductive success of the population, see Wickler (1973). In addition, special observations were carried out to study the effects of monogamy upon the individual.

First, we tried to find out whether seeking and maintaining proximity to the partner was part of the aggressive, sexual, or brood-care behavior system. There was, however, no correlation with any of the behavior patterns of these systems; further, there is no partner preference for aggressive or sexual behavior. So our motivation analysis showed that there must be a special "drive for attachment" in *Hymenocera*, with a marked tendency to reunite with the partner.

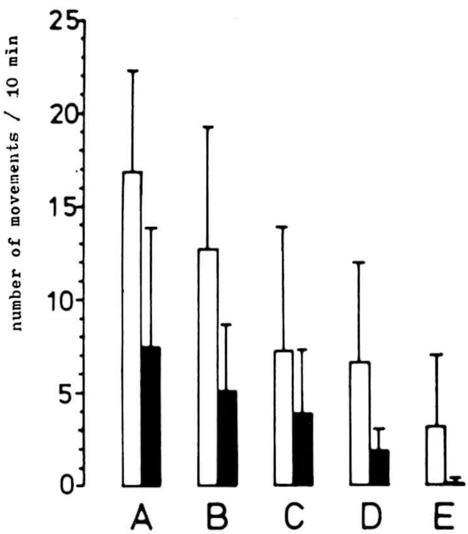

Fig. 3. Movements of isolated individuals (white bars) and animals sitting in pairs (black bars). Further explanation in text.

Secondly, there is a difference between pairs and single individuals in *Hymenocera* which has been seen by several careful observers. They called single individuals more "nervous" or more active than those sitting in pairs. To quantify this impression, we counted the number of movements (or the duration of a given activity) in individuals sitting either in pairs or sitting isolated. These counts (Fig. 3) did not include locomotion but other observable movements of the antennae (A), the big claws (C), the legs (D), the abdomen (E), as well as cleaning movements (B). Whichever behavior we chose gave the same results. Individuals sitting in pairs perform about half the amount of observable movements than do isolated individuals. The increase of activities in isolated animals of many different species has been interpreted as an indication of stress. Therefore, we suggest that attachment to a conspecific in *Hymenocera* is a means of reducing stress in the individual.

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FILMS[3]

E 1724 *Hymenocera picta* (Gnathophyllidae)—Fressen eines Seesternes. W. Wickler and U. Seibt 1971.

E 1725 *Hymenocera picta* (Gnathophyllidae)—Kopulation. U. Seibt 1971.

3 These films have been published through the Encyclopaedia Cinematographica and are available from the complete archives in a) Canada: Canadian Film Institute, National Science Film Library, 1762 Carling, Ottawa 13, Ontario; b) W.-Germany: Institut für den wissenschaftlichen Film, Nonnenstieg 72, D–34 Göttingen; c) Japan: EC Japan Archives, Shimonaka Memorial Foundation, Heibonsha Building, 4 Yonbancho, Chiyodaku, Tokyo; d) USA: The Pennsylvania State University, Audio-Visual Services, 6 Williard Building, University Park, Pa. 16802.