Reference: *Biol. Bull.* **187**: 274–275. (October, 1994)

Food Detection and Preferences of the Nudibranch Mollusc *Hermissenda crassicornis*: Experiments in a Y-Maze

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Hermissenda crassicornis (Eschscholtz, 1831), a nudibranch mollusc, is being reared in our laboratory as a biomedical research model for learning and memory studies. The aim of the present study was to determine whether *Hermissenda,* a generalist carnivore (1), is able to detect its prey chemotactically, and whether it displays a preference for certain foods. Previous studies on other nudibranchs demonstrated their ability to detect prey from a remote distance (2, 3).

Experiments were carried out in a 35 cm wide × 70 cm long × 12 cm deep Y-maze with a total equilibrated flow of 1500–2500 ml/min of ambient seawater (water depth: 3 cm each arm: 17 cm wide). A uniform, unidirectional flow was achieved with an upstream collimator made of soda straws. Dye tests confirmed the uniformity of the currents (*i.e.,* stimulus) across the full width of both arms of the maze.

The hydroid *Tubularia crocea,* the tunicate *Ciona intestinalis,* and the mussel *Mytilus edulis* were the foods tested. These species have all been used successfully in the past to feed *Hermissenda* in the laboratory (1, 4); *Ciona* was presented with the tunic removed, and mussels were presented without shells. Food was placed on one side of the Y-maze, with the other side remaining empty. For Y-maze experiments, *Tubularia* was presented whole; *Ciona* in three ways: whole, viscera only, and viscera cut into pieces; mussels were whole but without shells. In trials testing for a preference between stalks and polyps of *Tubularia,* the pieces of the hydroid were contained in 500-μm mesh bags, one on each side of the Y-maze.

Healthy *Hermissenda,* in groups of 3–6, were starved overnight before being tested. Individuals were selected at random from the starved group for each trial (1–3 non-consecutive trials/specimen). The nudibranch was placed on the centerline of the Y-maze, where it received stimuli from both sides (distance from the food barrier: 40 cm; 12–15 cm from the divider). The trial ended when *Hermissenda* was within 3 cm of the food barrier or after 30 min. The Y-maze was thoroughly cleaned between trials to remove the mucous trail of the previous specimen, and the maze was reconditioned by flushing for 10 min with ambient seawater between trials. Food was switched to the opposite side of the maze after 3–5 trials, and 33–56 trials were done with each food item. At least 50 *Hermissenda* individuals were used. About the same number of trials were done with the stimulus on the left and on the right; no significant bias was detected (χ^2). Results (number of times the side containing food was chosen *vs.* number of times the empty side was chosen) were compared by Chi-squared analysis.

Results of the Y-maze experiments are shown in Table I. In trials with *Tubularia,* when a choice was made, the nudibranchs went to the hydroid side in 72.5% of the trials (or 59% of the trials including no-choice data). When approaching *Tubularia,* a tendency for the pedal locomotion to accelerate in the last few centimeters was observed. The other foods gave much larger percentages of negative results (no choice made), whereas the results in which a choice was made were split about evenly between the presence and absence of food. When animals failed to make a choice, they crawled aimlessly or entered a quiescent state. For all foods tested, the average time for the nudibranchs to reach the finish line (when they made a choice) was between 6 and 16 min. Additional experiments with *Tubularia* were carried out at higher water temperatures; they also gave a large proportion (69%) of no-choice results. When stalks and polyps

Table I

Y-maze experiments with Hermissenda crassicornis *and various foods*

	Food chosen[a]	Blank chosen[a]	No choice[a]	n	χ^2
Tubularia (10–12°C; 17–19°C)[b]	59% (29)	22% (11)	18% (9)	49	8.10[c]
Tubularia (24°C)	31% (5)	0%	69% (11)	16	—
Ciona (whole) (20–23°C)	5% (2)	16% (6)	79% (30)	38	2.0
Ciona (viscera whole) (20–24°C)	11% (4)	8% (3)	81% (29)	36	0.14
Ciona (viscera pieces) (20–24°C)	17% (6)	9% (3)	74% (26)	35	1.0
Mytilus (22–24°C)	6% (2)	9% (3)	85% (28)	33	0.2
	Polyps chosen	**Stalks chosen**	**No choice**	**n**	**χ^2**
Tubularia (19–21°C) (polyps vs. stalks)	34% (19)	38% (21)	29% (16)	56	0.1

[a] Results are given in rounded percentages. (n) = Number of trials.
[b] The data from these sets of experiments, done at two temperature ranges, were combined because they were not statistically different (χ^2).
[c] Statistically significant ($P = 0.005$; d.f. = 1). Remaining χ^2 values were not significant.

of *Tubularia* were presented simultaneously, the nudibranchs went to the stalks as often as to the polyps (Table I).

This study demonstrates that *Hermissenda* can locate *Tubularia* by chemotaxis. Previous reports (5, 6) indicated that this nudibranch can locate dissolved food at a distance in the laboratory, but not solid food. In those studies, however, the nudibranchs were not tested with unidirectional water currents passing over food species. *Hermissenda* did not distinguish between hydroid polyps or stalks in the Y-maze, choosing equally between the two. Although they do eat the other tested foods in the laboratory, they were not strongly attracted to them in the Y-maze experiments. Entire *Ciona* may actually be repellent. This fact might be related to the presence, in *C. intestinalis,* of a cytotoxic steroidal hydroperoxide (7, 8). Feeding experiments done previously with adult *Hermissenda* showed that a diet of *Tubularia* sustained a higher growth rate than diets of *Ciona* viscera or mussels. These results reinforce the fact that the latter two foods are useful only as maintenance diets (9).

High percentages of negative trials (no choice expressed) in similar chemotactic experiments have been reported in the literature, putatively due to variability in the animal's physiological state and environmental conditions (3). In our experiments, negative results (no choice) increased in direct relationship to seawater temperature (Table I). A water temperature of 24°C greatly exceeds the normal temperature range for *Hermissenda.* Because *Tubularia* is also a natural inducer of larval metamorphosis, detection and selection of the hydroid as preferred prey can be ecologically critical to *Hermissenda,* by increasing the rate of larval and juvenile survival.

Financial support from the Woods Hole Marine Sciences Consortium to E.T. and the Catalan and Spanish Governments to C.A. are gratefully acknowledged. This research was supported by a grant to A.M.K. (N.C.R.R.-N.I.H.; P40-RR03820). Thanks are also due to Dr. J. Atema and Dr. R. Voigt for lending us the Y-maze for our experiments. Technical support of C.T. Tamse is also acknowledged.

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Reference: *Biol. Bull.* **187:** 275–276. (October, 1994)

Aggression-Reducing Courtship Signals in the Lobster, *Homarus americanus*

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Shelters are very important for lobster social behavior. Males defend shelters (1), and dominant males in large "mating" shelters are more likely to mate (2). Females enter such occupied "mating" shelters and cohabit for about two weeks, during which time they molt and mate (3). Intermolt, transient matings have also been reported (4). The latter have been observed only in artificial laboratory conditions, but they do suggest multiple mating strategies.

This paper examines male and female entry of occupied shelters, and the postural and chemical signals used to communicate with the resident male. All experiments were carried out in a 3.7-m, Y-maze flume with a mating shelter in each arm. Seawater entered behind each shelter, flowed down each arm and through each shelter at 1.0 cm/s, and drained through a standpipe placed downstream at the other end of the flume. Two different dominant males were used throughout the experiment. A test began by placing one of the dominant males in one of the shelters, fitted with a transparent top. The other shelter was left empty. The test animal was placed behind a gate downstream near the standpipe. After 10 min the gate was removed and the animal allowed to move throughout the flume for 15 min. A camera over the flume, and another over the shelters, allowed observation of the visiting animal's movements in the flume and behaviors inside the shelter. Ten mature males and 15 mature females were tested. All experiments were conducted during the dark phase of a 14:10 light cycle. The flume was illuminated by dim incandescent bulbs, and the shelters by a red photographic safelight. Visiting animals were tested with and without an attached nephropore catheter, which collects urine, preventing its release into the water.

Of the 10 visiting males tested, 8 attempted to enter the occupied shelter. The resident male resisted, primarily by pushing with his claws. Occasional bouts of higher level aggression, such as claw lock (seizing an opponent with one claw), scissoring (rapidly crossing closed claws), and snapping (ripping an opponent with claws) were seen. Four of the five successful entering attempts required eviction of the resident. Blocking urine release had no significant effect upon resident male or visiting male behavior, or the visiting male's ability to evict the resident.

Females of all molt stages also attempted to enter the male-occupied shelter (13 of 15 tested), but the resident male's reaction was quite different. In all but two cases the females were allowed