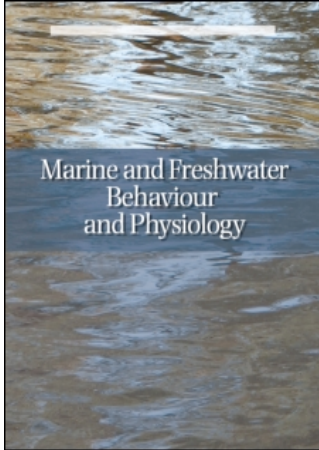


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## INDIVIDUAL DISCRIMINATION IN THE BIG-CLAWED SNAPPING SHRIMP, *ALPHEUS HETEROCHELIS*

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Rahman *et al.* (Rahman, N., Dunham, D.W. and Govind, C.K. (2001). Mate recognition and pairing in the big-clawed snapping shrimp, *Alpheus heterochelis*. *Mar. Fresh. Behav. Physiol.*, **34**, 213–226.) demonstrated discrimination by snapping shrimp between former mates and unfamiliar conspecifics, but did not test individual discrimination. In the present study, snapping shrimp showed discrimination between familiar and unfamiliar same-sex conspecifics by preferentially entering that arm of a Y-maze leading to familiar individuals. Furthermore, after being exposed to water from the home tanks of unknown individuals, they later showed an elevated response to this water, if the direction from which the water came into their tank was changed to be novel. This indicates that test subjects associated a familiar chemical stimulus with its location in the environment. This discrimination could only have been made if that chemical signature were recognised as different from that of another chemically familiar individual. This result also demonstrates that the water surrounding an individual contains sufficient (chemical) information to allow discrimination of one individual from another.

*Keywords:* *Alpheus*; Snapping shrimp; Individual recognition

### INTRODUCTION

Individual recognition in invertebrates is not well studied. In crustaceans, mate recognition studies are uncommon, despite the fact that monogamous pairing occurs in stenopid, gnathophyllid, alpheid, and crangonid shrimp, and in isopods. Desert isopods show individual recognition, probably based on chemical cues (Linsenmair and Linsenmair, 1971). Seibt and Wickler (1972) demonstrated that *Hymenocera picta*, the clown shrimp, is capable of individual recognition, and Johnson (1977) found recognition of former mates in the banded shrimp, *Stenopus hispidus*. Caldwell (1979, 1982, 1985) showed that several stomatopod species are able to recognise individuals and demonstrated that *Neogonodactylus bredini* displayed reduced aggression towards

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former mates (Caldwell, 1992). Atema and co-workers showed individual recognition in the Atlantic lobster, *Homarus americanus*, and explored its role in social structure (Karavanich and Atema, 1998).

We will use the term 'discrimination' below to mean a difference in response to two stimuli. Where the stimuli emanate from different individuals, we will describe this differential response as discrimination between those individuals.

Rahman *et al.* (2001) tested discrimination between former mates and unfamiliar conspecifics by male and female snapping shrimp, *Alpheus heterochelis*. This was a test of discrimination based on familiarity, but not a test of individual discrimination. They found significant differences between the acts performed by former mates and those performed by strangers. It was inferred that this discrimination was based on information gained from the interaction of a cohabiting pair, but the nature of the information was not identified.

In the present laboratory study, we continue this line of investigation, using animals of the same species and field population as in the above study. We evaluate the response of individuals to others with whom they are familiar, and to strangers. We use the relative location of chemically familiar stimulus individuals in the immediate environment as a variable to test the ability of our subjects to discriminate one chemically familiar stimulus individual from another.

## METHODS

Animals were obtained from the Duke University Marine Laboratory in Beaufort, North Carolina and maintained at the University of Toronto. The animals were kept in 25-L aquaria (41 × 20.5 × 26 cm deep) partitioned by plastic screening into 12 compartments for individuals. This made possible chemical interaction among the animals, but restricted visual contact and precluded physical contact. Aquaria contained 'Instant Ocean' brand synthetic salt water (specific gravity 1.023), gravel to a depth of approximately 2 cm, and were equipped with an under-gravel filter. The same salt-water mixture and gravel substrate were used in the other containers as well. Shelters, where provided, were black plastic cylinders (10 cm long and 2 cm in diameter), unless stated otherwise. The animals were fed Purina brand 'Trout Chow' daily, and maintained at 28°C under a light-dark cycle of 18–6. Only intermoult animals were used in this study.

Size-matched, and mismatched, animals were classified by placing individuals in small Plexiglas cuvettes, and then viewing them together, two at a time. Those pairs whose body and major chela length differences could not be detected by eye were considered to be size-matched. Mismatched pairs were similarly estimated by eye to differ by 10–30%. Our experimental population ranged from 32 to 38 mm in body length and 14–18 mm in major chela length.

Both the focal and stimulus animals in any given experimental replicate were of the same gender. Experiment 1 comprised seven female replicates and six male replicates, and Experiment 2 comprised six female replicates and eight male replicates. The outcomes of female and male replicates were not different (*T* values ranged from 35.000 to 45.000 and *P* values ranged from 0.366 to 0.945), so the data were combined for analysis.

## Experiment 1

### *Procedure*

The purpose of this experiment is to determine whether a focal animal can discriminate between a familiar and an unfamiliar conspecific (outside of a mating paradigm). Two size-matched stimulus animals were isolated for 24 h in clear, 500 mL Plexiglas containers ( $10.5 \times 6.5 \times 9.5$  cm deep) containing a clear glass vial shelter (length 5.5 cm, mouth 1.9 cm, diameter 2.5 cm). Next the focal animal and one larger stimulus animal were placed in a 25-L tank ( $51.5 \times 25.5 \times 30.5$  cm deep). In no case had the focal animal been previously housed with either stimulus animal. The two shrimp interacted for 30 min, and their behaviour was recorded. Lunges and snaps with the major chela were collectively tallied. The animal that performed more of these, by a count difference of eight or greater, was considered dominant. Dominance was always unambiguous by this criterion. The larger individual invariably became dominant over the smaller animal, usually within the first 10 min.

Then the dominant animal was placed in a chamber at the end of one of the two arms of a Plexiglas Y-maze (see Fig. 1). The unfamiliar larger animal was placed in the end chamber of the other arm, or that chamber was left empty. These two treatments were alternated sequentially between replicates, as was the side of the maze containing the dominant animal. The chambers were separated from the rest of the arm by a partition comprising two offset layers of fine, black plastic screening, making the partition almost opaque, but allowing a flow of water through it. A water inflow tube (3 mm in diameter) entered the end of each arm and the water outflow tube (6 mm in diameter) exited the end of the base. The direction of gentle water flow through the two arms and out the base of the Y-maze prevented the diffusion of water from either arm into the other arm, as was previously determined by dye tests.

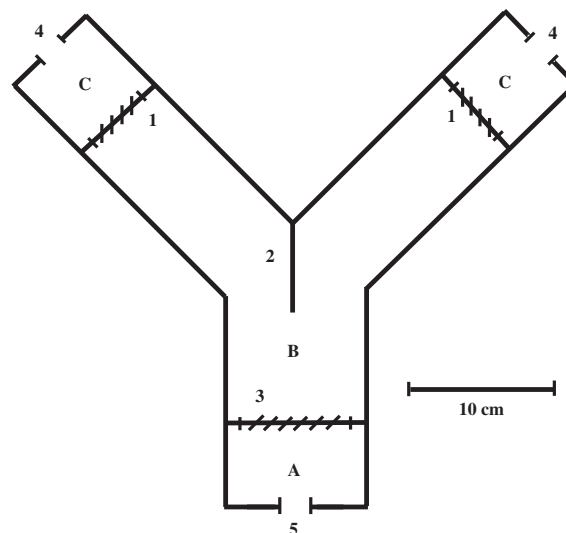


FIGURE 1 The Y-maze used in experiment 1. Chambers C housed the stimulus animals, behind mesh partitions (1). Chamber A initially held the focal animal, behind a removable mesh partition (3). 4s denote the water inflow tubes and 5 the water outflow tube. B is the area in which a choice was made by moving past the semi-partition (2). The inside tank depth was 9.5 cm.

The focal subordinate animal was placed in the chamber at the bottom of the base, behind a removable mesh partition. After 5 min the water flow was started and the partition separating the focal animal from the rest of the maze was removed, giving it access to the two arms, or the option of remaining in the base chamber. The floor area of the base was larger ( $117 \text{ cm}^2$ ) than the floor area of an arm ( $103 \text{ cm}^2$ ). Its behaviour was recorded for 10 min. The focal animal was then returned to the base chamber and the mesh barrier replaced. The familiar dominant stimulus animal was moved to the opposite stimulus arm chamber, and the complementary stimulus to that in the first trial, either no stimulus animal or the unknown animal, presented in the other arm chamber. After 5 min the same procedure as in the first trial was repeated.

The data recorded were total time the focal animal spent in each stimulus arm, the frequency of entering each arm, the frequency of climbing on the mesh barriers, the frequency of inserted walking legs through the mesh barriers and frequency of pulling at the mesh barriers with the pincer claw (minor chela). This experiment was performed 13 times ( $N = 13$ ).

## Experiment 2

### Procedure

The purpose of this experiment is to determine whether a focal animal discriminates chemically between two familiar animals. Two stimulus animals were sized matched to each other and to the focal animal, and isolated in separate 1-L glass tanks ( $16 \times 16 \times 16 \text{ cm}$ ), containing a shelter, for 48 h. At the same time the focal animal was isolated in a 500-mL clear Plexiglas container ( $10.5 \times 6.5 \times 9.5 \text{ cm}$  deep) with a clear glass vial shelter (length 5.5 cm, mouth 1.9 cm, diameter 2.5 cm). In no case had the focal animal been previously housed with either stimulus animal.

The two stimulus animal tanks were positioned 1 m above the experimental tank (see Fig. 2), and were not disturbed in any way for 24 h prior to the experiment.

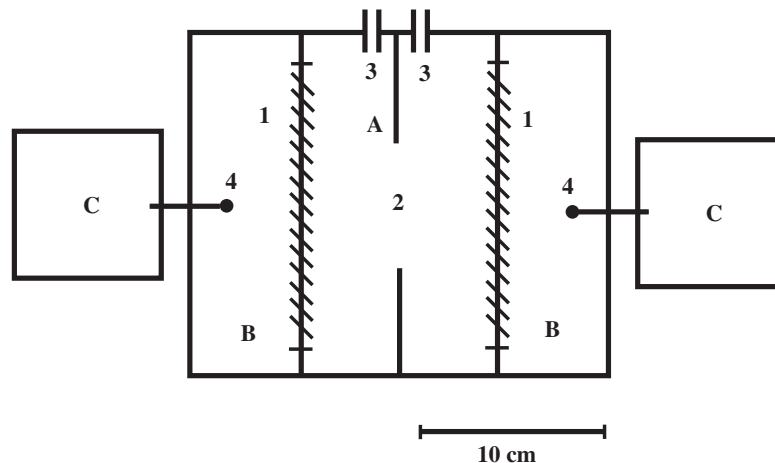


FIGURE 2 The testing tank used in experiment 2. A indicates the semi-partition in the central chamber (2) and B are the side chambers, separated from the central chamber by black mesh screens (1). 4s denote positions of burettes and inflow from the stimulus tanks (C). 3s show the outflow tubes. The inside tank depth was 17 cm.

The experimental tank was clear Plexiglas, and comprised a central chamber, separated from two flanking chambers by black plastic mesh. The central chamber was further divided by two clear Plexiglas semi-partitions that forced the focal animal to pass through a gap between them when moving from the half of the central chamber nearer one flanking chamber to that nearer the other, and vice versa. Prior to experimentation a 90-mL burette was positioned 5 cm above the water surface of each flanking chamber. These were connected by plastic tubing to the respective tanks of the stimulus animals, providing a continuous drip into the flanking chambers, one drop per sec, from the two sources of stimulus water. Previous dye tests showed that stimulus water reached the mesh partitions in 3 min at this drip rate.

After the initial 48-h isolation, the focal animal was placed in the central compartment of the experimental tank, and the burettes were turned on. After a 3-min pause, the frequencies of behaviours directed towards either mesh screen were recorded for the next 27 min. These were the initial data.

The behaviours recorded were: *Fan* – this was counted as the number of waves of pleopod movement down the length of the animal; *Groom* – stroking of carapace or pleopods with the pereopods; *Antennal Contact* – touching or moving one or both second antennae against the screen; *Climb* – the entire body moves up to a vertical position against the screen; *Pull* – the pincer claw (minor chela) pulls on the mesh material; *Leg Poke* – one or more pereopods are inserted into holes in the mesh.

After recording these initial data, the focal animal was left in the experimental tank, with continued stimulus inflow from the burettes, for 2 h. Then the same measures were again recorded for 27 min. These were termed the pre-experimental data. Next, the two burettes were removed and immediately repositioned, either where they were initially (control treatment), or on opposite sides, replacing each other (experimental treatment). After 3 min the same measures were recorded for 27 min. Last, burette removal and repositioning were performed again, with the complementary manipulation. Thus each focal animal was tested under the two treatments, but half experienced the control manipulation first and half the experimental manipulation first. This experiment was performed 14 times ( $N = 14$ ).

## RESULTS

Data from Experiment 1 were analysed with Mann-Whitney Rank Sum Tests, and the data from Experiment 2 were analysed with Kruskal-Wallis One Way Analysis of Variance on Ranks ( $df = 3$ ), followed by Student-Newman-Keuls Pairwise Multiple Comparison Procedure (at an alpha error level of 5%), all performed with Jandel Sigma Stat version 2.0 software.

In Experiment 1, the Y-maze tests showed significantly more time spent by the focal animal in that arm that contained the known and dominant individual, than in the empty arm ( $T = 231.00$ ,  $P = 0.005$ ) or the arm containing an unknown individual ( $T = 223.00$ ,  $P = 0.016$ ) (see Fig. 3). There was no significant difference in the time spent in the empty arm *versus* the arm with the unknown individual ( $T = 160.000$ ,  $P = 0.442$ ).

The frequency of approaches to the compartments in the two arms showed the same pattern. The compartment containing the known, dominant individual was approached more frequently than either the empty compartment ( $T = 218.500$ ,  $P = 0.029$ ) or that

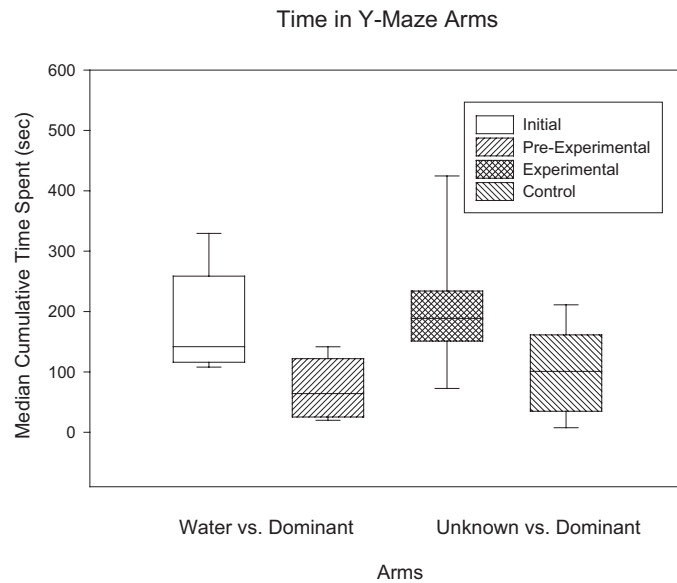


FIGURE 3 The median time spent in each arm of the Y-maze by the focal animal in experiment 1. Dominant is the arm with the dominant, known, individual. Water is the arm containing only water. Unknown is the arm with the unknown individual. The choices are indicated as *vs*. The medians, 25 and 75% quantiles, and ranges are shown.

containing the unknown individual ( $T=217.00$ ,  $P=0.035$ ). There was no significant difference in the frequency of approach to the known animal's compartment across tests ( $T=193.500$ ,  $P=0.369$ ), or to the empty *versus* the unknown's compartment ( $T=181.000$ ,  $P=0.798$ ).

In Experiment 2, four categories of contact with the mesh screens, Antennal Contact, Climb, Pull and Leg Poke, were measured. Fan and Groom were also monitored. Measurements were made in the initial and pre-experimental periods, and then under both the experimental and control treatments. Grooming frequency was much lower in the initial period than in the subsequent periods ( $H=28.176$ ,  $P < 0.001$ ). All of the other five behaviours occurred more in the initial period than in the subsequent periods ( $P < 0.05$  for all). Antennal Contact, Leg Poke and Pull occurred more frequently in the experimental treatment than in the control ( $P < 0.05$  for all). Pre-experimental and control frequencies did not differ significantly for these acts ( $P > 0.05$  for all). Climb and Groom frequencies did not differ significantly between experimental and control treatments ( $P > 0.05$  for both). [See Fig. 4 for Antennal Contact and Table I for the other acts.] The frequencies of the acts did not differ significantly between tests where the experimental treatment preceded the control treatment and those where the reverse order was used ( $T$  values ranged from 43.000 to 60.000 and  $P$  values ranged from 0.259 to 1.000).

## CONCLUSIONS

The results of Experiment 1 show that *A. heterochelis* can discriminate between a familiar conspecific and an unfamiliar one, as was shown previously for this species

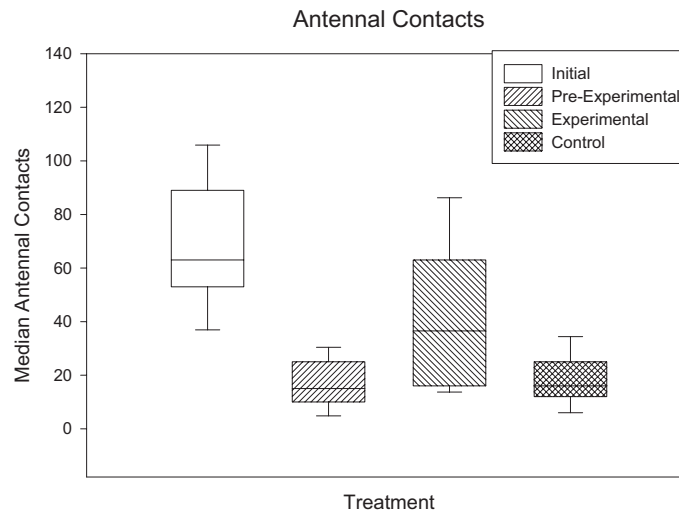


FIGURE 4 The median number of Antennal Contacts with the screen partitions in experiment 2. The medians, 25% and 75% quantiles, and ranges are shown for each of the four treatments.

TABLE I Act frequencies from experiment 2. **Medians** [25th–75th quantiles]. *P* values from Student-Newman-Keuls pairwise multiple comparisons

Behaviour	Initial	Pre-experimental	Experimental	Control	Exp. vs Control <i>P</i> < 0.05
Antennal contact	<b>63</b> [53–89]	<b>15</b> [10–25]	<b>36.5</b> [16–63]	<b>16</b> [12–25]	Yes
Fan	<b>134</b> [99–155]	<b>13.5</b> [2–40]	<b>38.5</b> [21–69]	<b>16</b> [6–37]	Yes
Pull	<b>28</b> [19–48]	<b>0</b> [0–3]	<b>4.5</b> [1–13]	<b>0.5</b> [0–2]	Yes
Leg poke	<b>60</b> [37–73]	<b>17</b> [10–34]	<b>47</b> [29–55]	<b>11</b> [6–30]	Yes
Climb	<b>39</b> [33–47]	<b>9</b> [5–15]	<b>15</b> [7–23]	<b>11</b> [6–12]	No
Groom	<b>1</b> [0–3]	<b>21.5</b> [18–33]	<b>17.5</b> [13–24]	<b>24</b> [17–32]	No

(Rahman *et al.*, 2001), but is here first shown in a non-mating context. We also demonstrated that this discrimination can be made on the basis of chemical information. What we did not expect to find was an attraction by the subordinate animal to the dominant one; we had expected avoidance. This suggests that the agonistic bouts did not confer sufficient negative reinforcement to preclude further initiation of interaction by the subordinate individual. We did not test that directly, since the animals could not subsequently interact physically in our testing environment.

In Experiment 2, the comparison of initial data with pre-experimental data generally showed a decrease in activity, with the exception of Groom, over a 2-h period following the introduction of the focal animal to the two odour sources. We interpret this to be a result of familiarity with the initially novel physical and chemical environment of the ‘neighbourhood’. The pre-experimental data subsequently served as a baseline against which activity during the experimental and control treatments could be compared.

Experiment 2 showed that *A. heterochelis* can associate different ‘odours’ with different locations in the immediate surround. Three categories of contact with the mesh screens, Antennal Contact, Pull, and Leg Poke, were significantly elevated if the location of familiar water entry was changed. The screens were the partitions separating the

focal animal from the odour sources. Antennal Contact brings both the first and second antennae into close proximity to an odour source. Crustacean antennae have been shown to bear sensilla that transduce water borne chemical information (Hallberg *et al.*, 1997). Fan with the pleopods was similarly elevated. This produces a current, which increases gill ventilation, and has been shown in other crustaceans to mediate dissemination of pheromones in a social context (Atema, 1986). General climbing behaviour (Climb) and Groom, an activity used in care of the body surface, did not show this change.

We have shown that a change in the location from which an odour diffuses causes an increase in the frequency of several acts performed by the focal animal. Since a change in location can only be detected if the subject discriminated between the two odours presented, this demonstrates discrimination between the chemical 'signatures' of two individuals. We can conclude that *A. heterochelis* can discriminate between two known, same-sex individuals, and that it can do so on the basis of chemical information.

A formally similar paradigm has been used in many ornithological field studies of the response of songbirds to playback of neighbour song from familiar and novel locations, since the pioneering work of Lanyon and of Falls (Falls and Brooks, 1975).

### Acknowledgements

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