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Chemical cues and binary individual recognition in the hermit crab *Pagurus longicarpus*

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Abstract

The behaviour exhibited by the hermit crab *Pagurus longicarpus* in response to an empty shell varied in the presence of cues from conspecific individuals according to its familiarity or not with them. This binary discrimination was independent of the conspecific's relative size and was based on chemical signatures, an ability that this species shares with a few other aquatic invertebrates. From our results, olfaction appeared to be the dominant sensory channel in *P. longicarpus*' binary discrimination, but the combination of two signal components from visual and olfactory channels resulted in the enhancement of the response displayed by the receiver. Besides, crabs reacted differently when exposed to their own odour than to the odour of familiar (as well as unfamiliar) conspecifics, suggesting that recognition in this species can be more refined than a binary discrimination and that chemical 'badges' may be attributes of individual crabs.

Key words: individual recognition, chemical cues, multimodality, hermit crabs, *Pagurus longicarpus*

INTRODUCTION

Since Wilson's (1970) claim that individual identification may be one important and common message of pheromones, there is now greater awareness of the fact that odours enable conspecifics to identify one another under various social contexts, such as mother–offspring relationships, mated pairs, dominance hierarchies and group membership (Shorey, 1976).

Much has been learned about chemically-mediated mechanisms of individual recognition in vertebrates (Halpin, 1980) and several notable findings have been reported in the study of non-human mammals (e.g. Halpin, 1986; Brown, Roser & Singh, 1990; Hurst *et al.*, 2001). A plethora of studies has been directed to characterize the process of the sender signalling its identity (identification; Beecher, 1989), the process of the receiver extracting information about identity (recognition; Beecher, 1989), and the adaptive functions of both identification and recognition (Halpin, 1986), as well as the nature of individual representations (Johnston & Bullock, 2001) and their evolutionary pathway (Halpin, 1986).

To date, a relatively small body of literature exists on the above issues in invertebrates (see, e.g. Leonard, Ehrman & Schorsch, 1974 and Ehrman & Probber, 1978 in *Drosophila* spp.; Barrows, 1975 and Barrows, Bell & Michener, 1975 in halictid sweat bees *Lasioglossum zephyrum*; Liechti & Bell, 1975 in the cockroach *Byrsotria fumigata*; Linsenmair & Linsenmair, 1971 in the desert wood loose *Hemilepistus reaumuri*). Few studies have shown that pheromones enable individual recognition in aquatic invertebrates (Wickler & Seibt, 1970 in the clown shrimp *Hymenocera picta*; Johnson, 1977 in the banded shrimp *Stenopus hispidus*; Caldwell, 1979 and 1985 in the mantis shrimp *Gonodactylus festae*).

Research has been obviously hampered by the difficulty in finding a method that could investigate reliable responses to chemical cues and that could furnish a measure of one or more activities allowing for quantitative analyses. As an example, Caldwell (1985) recorded the time *G. festae* intruders took to enter cavities containing water from the home cavity of dominant and subordinate individuals. One weakness of the methods used is that one can only demonstrate the ability of animals to classify conspecifics into three subgroups (e.g. unknown individuals and known individuals that either defeated the recognizing animals or were defeated by them, as in the case of *G. festae*) or most often into two subgroups (e.g. individuals that were either familiar or unfamiliar for the recognizing animals).

Because of these methodological constraints, we cannot determine whether an animal discriminates one individual of a group from every other individual on the basis of 'a unique set of cues defining that individual' (Beecher,

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1989), but at best we can categorize individuals into 'heterogeneous subgroups' (Barrows *et al.*, 1975). In other words, we are not able to demonstrate a 'true individual recognition' but a 'binary discrimination' among individuals (Boal, 1996). However, as pointed out by Barnard & Burk (1979), the distinction between true individual recognition and other apparently simpler forms of individual discrimination seems fallacious, because recognition acts on 'a continuous scale of cue complexity ranging from simple cues to complexes possibly beyond the level of the individual'.

There are several reasons that make hermit crabs good subjects to examine mechanisms of individual recognition mediated by chemical cues in aquatic invertebrates. First, individual recognition maintains dominance hierarchies in *Pagurus bernhardus* (Hazlett, 1969); recently, Gherardi & Tiedemann (2004) demonstrated the existence of a binary individual recognition between *Pagurus longicarpus* opponents. Second, the olfactory environment where hermit crabs live seems complex enough to justify the potential to chemically recognize conspecifics. Several hermit crab species display adaptive responses when exposed to chemicals that signal shell availability (either chemicals associated with gastropod tissue odours, Rittschof 1980, or conspecific hemolymph, Rittschof *et al.*, 1992), this behaviour depending on the inhabited shell fit (Katz & Rittschof, 1993) and being affected by predator odours (Rittschof & Hazlett, 1997). Third, when offered empty gastropod shells, crabs perform a series of investigatory acts (Elwood & Stewart, 1985; Jackson & Elwood, 1989), during which they assess external and internal features of the shell and then make a decision on whether or not to enter it. As shown in other studies (Hazlett, 1996*a*,*b*; Rittschof & Hazlett, 1997; Hazlett, 2000) and confirmed here, the detection of odours affects the response towards shells either inhabited by conspecifics (previous studies) or empty (this study). Therefore, the behaviour of hermit crabs in response to empty shells seems to provide a means to investigate chemical recognition.

Based on the above premises, the objective of this study was to explore the role that the detection of chemical cues exercises in the binary discrimination of conspecifics by the long-clawed hermit crab *P. longicarpus*. Because animal communication frequently involves multiple signals delivered simultaneously in different sensory modalities and, as it was observed at least in snapping shrimp (Hughes, 1996), concurrent signals emitted by the sender may provide additional or modifying information to the receiver, we also analysed the potential effects on individual recognition of either visual stimuli alone or visual plus chemical stimuli.

MATERIALS AND METHODS

Subjects, collection and housing conditions

In July–August 2002, 350 *P. longicarpus* Say 1817 with a shield length of 4–6 mm were hand-collected haphazardly from muddy/sandy areas of the Sandy Hook peninsula (New Jersey, USA) during diurnal low tides. Immediately after the capture they were separated into small groups. In the laboratory, the specimens were maintained in groups of up to 25 individuals for no more than 2 weeks until used in a temperature-controlled room (22 °C) and under a 14L:10D cycle. They were kept in separate 20-l holding aquaria containing constantly aerated, artificial seawater (Instant Ocean^{TM} salts) at the salinity of natural seawater (27 ppt) and fed a diet of commercial shrimp pellets every third day. Water was changed weekly. After being used in experiments, the crabs were released back into the collection site.

Preliminary free-choice experiment

To avoid any effect of shell species, size, quality and fit on *P. longicarpus*' agonism in the first experimental session and to make the motivation for obtaining a new shell as similar as possible in the second experimental session, crabs were given a choice of shells from a number (5 per hermit) of empty, unfouled and undamaged *Ilyanassa obsoleta* shells ranging in size from 5 to 20 mm in aperture length (following Angel, 2000) and having a colour as uniform as possible. These were prepared by collecting live *I. obsoleta* (the dominant shell type used by the study population), boiling and removing the flesh, rinsing in seawater, and air-drying. Crabs were allowed 48 h of free access to shells. The shells occupied at this time were assumed to be of preferred size since the crabs had ceased exploring and moving into new shells.

Experimental protocol

The experiment comprised 2 sessions of observation. The first was aimed at defining dominance within each pair of crabs, while in the second session we compared the reaction of test crabs towards a novel, empty, and optimal shell of *I. obsoleta* (hermit crabs, even inhabiting optimal shells, have the tendency to approach novel shells). Crabs were tested in 3 different contexts, where test animals could (1) see only, (2) smell only, or (3) see and smell 1 conspecific. Conspecifics were either known (familiar conspecifics, FC) or unknown (unfamiliar conspecifics, UC) individuals that, however, were of the same status (dominant or subordinate) as the former opponents. A distinction by status appeared necessary because previous studies on other decapods (e.g. lobsters, Breithaupt & Atema, 2000; crayfish, Zulandt Schneider, Huber & Moore, 2001) showed that, once a hierarchy was formed, opponents were able to recognize each other from urine scents of the dominant (and/or of the subordinate) status. As controls, we recorded the responses towards the shell of test crabs in the absence of any stimuli emitted by 1 conspecific (but in the presence of the test crab's odour alone). In both sessions, crabs were kept in plastic bowls containing 160 ml artificial seawater at the salinity of natural seawater (27 ppt) and at 22 °C temperature; bowls were visually isolated from each other and

kept within a uniformly coloured (white) substrate and background. During observations, which were performed between 09:00 and 16:00, bowls were illuminated by a 75-W overhead incandescent light, 50 cm over the water level.

We formed 160 pairs by taking at random individuals with no missing limbs from each separate holding aquarium to ensure they had no prior knowledge of one another. Crabs were size-matched (the major chela differed by $< 5\%$ in length between the individuals of each pair) to reduce any influence of size on dominance. Sex was not noted since sex has been shown to exert no effects on agonistic interactions in this and other hermit crab species (Winston & Jacobson, 1978). No mating behaviour was ever observed during this study, reproduction occurring between October and May with a peak in autumn (Wilber, 1989). The shells inhabited by crabs were marked by 1 or 2 dots of permanent black ink, while crabs were recognized by the length of their antennae and by slight differences in cheliped and walking leg colour.

Session 1

In the first session, pairs were observed after 24 h of cohabitation. This session allowed us to identify dominant (alpha) and subordinate (beta) opponents. Based on Winston & Jacobson's (1978) data, 24 h were sufficient for the formation of a dominance hierarchy in this species. However, 30 min before starting the second session, we always checked for the status of each individual (that did not change in any pair) and recorded those shell switches (in 10 pairs) that had occurred overnight.

Immediately preceding observations, the members of each pair were removed from their bowl, and after a few seconds were introduced onto a different bowl containing clean seawater on opposite sides of a removable, opaque plastic sector. After 5 min of acclimation, the divider was lifted and the crabs were allowed to interact with each other.

During 15 min of observation we tape-recorded variables that describe aggression in crabs, that is: number of interactions, types of interactions (distinguished into avoidance, threat, contact, exploration, and shell fight, each ranked on a scale of intensity of 1 to 5; Gherardi & Tiedemann, 2004); average score (obtained dividing the sum of the interaction intensities for each pair within 15-min observations by the number of interactions); latency (the time passed between the beginning of our observations and the start of the first interaction; when no interactions occurred we arbitrarily assigned a latency time of 905 s); and the winner and thus dominance (the percentage of interactions won by the dominant individual on all interactions). We deemed as alpha the individual that was the winner of more than half of the interactions. At the end of every observation, pairs were maintained in the same bowl where they had interacted and kept under the same conditions as in the first day of cohabitation.

Session 2

The second session was run 24 h after the first session. Each pair was randomly assigned to 1 of the 3 experimental treatments or to 1 of the 2 control trials. Overall, we tested 80 different crabs (40 alphas and 40 betas) for each treatment or control trial. The test apparatus consisted of opaque, plastic bowls as described above, divided into 2 equal compartments by either a transparent (TR) or an opaque (OP), fixed plastic sector.

In experimental treatments, observations started by inserting the test crab and the non-test crab onto the opposite compartments of the apparatus. The compartment where the test crab was inserted contained a novel, empty shell of *I. obsoleta* placed with its aperture upwards; the test crab was put about 8 cm from it. The novel shell was prepared as described for the preliminary free choice experiment and was judged suitable for the test crab's size using the equation provided by Angel (2000) for the same species. The non-test crab was either the former opponent (FC) of the test crab or an unknown conspecific (UC) that was of the same status as the former opponent. Treatments differed for: (1) the sector that divided the test apparatus into 2 compartments that was either TR or OP; (2) the seawater contained in the compartment where the test crab was inserted. Seawater was conditioned with either the test crab's smell only (OWC) or the opponent's smell (OPC) by keeping the corresponding hermit crab in a 80-ml plastic bowl for 1 h. In the 'sight only' treatment, seawater was OWC and the sector was TR, thus the test crab could see, but not smell, the conspecific. In the 'smell only' treatment, seawater was OPC and the sector was OP, thus the test crab could smell, but not see, the conspecific. In the 'sight and smell' treatment, seawater was OPC and the sector was TR, thus the test crab could both see and smell the conspecific. Two control trials were run with seawater OWC and either a TR or an OP sector, but in the absence of any conspecific's cue ('none' trials). During 5 min of observation, we tape-recorded variables that describe the reaction of the test crab to the shell, that is:

(1) number of approaches to the shell;
(2) types of contacts with the shell, distinguished into avoidance (i.e. the test crab approached the shell but avoided it without any contact), physical contact (i.e. the test crab touched the shell with the antennae or chelipeds or walking legs), exploration (i.e. the test crab explored the external features of the shell with a series of movements of the chelipeds or its aperture through insertion of 1 or more thoracic appendages and/or rocked it back and forth), and shell switch. For the description of shell investigation we followed Elwood & Stewart (1985) and Jackson & Elwood (1989);
(3) latency, i.e. the time passed between the insertion of the test crab onto the apparatus and its first approach to the shell; when the test crab never approached the shell, we arbitrarily assigned a time of 305 s;
(4) the overall time spent by the crab interacting with the shell (duration of contact with the shell).

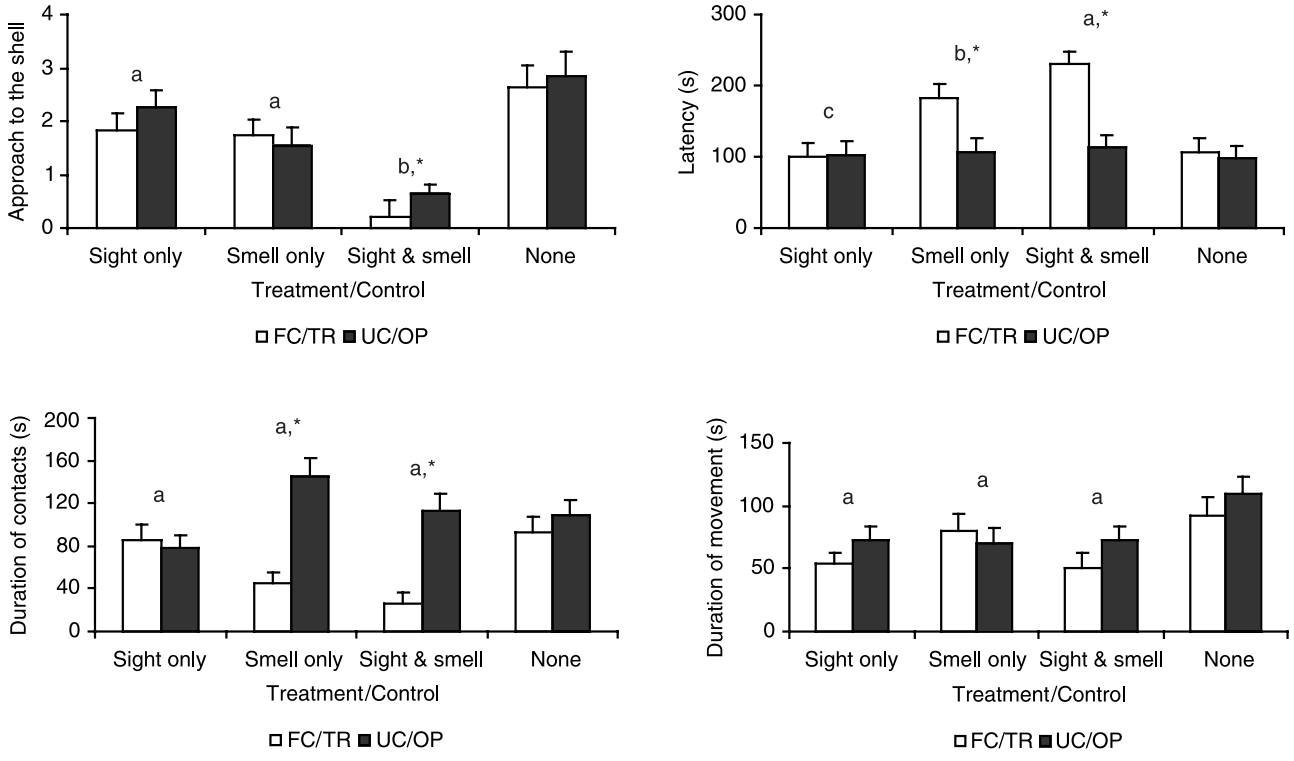

Fig. 1. Mean (+ SE) approach to the shell, latency, duration of contact with the shell, and duration of movement compared between familiar and unfamiliar conspecifics (FC and UC) in the three treatments of the second experimental session ('sight only', 'smell only', and 'sight and smell') and between transparent and opaque sectors (TR and OP) in the control. For each variable, N are 40 for FC/TR and 40 for UC/OP. Letters indicate the hierarchy among treatments; asterisk, significant difference between conditions (at least, $P < 0.05$). See Table 1 for the statistical output.

As an index of general activity, we also measured the overall time spent by the test crab moving in its compartment without interacting with the shell (duration of movement).

Statistical analyses

We followed the procedures found in Sokal & Rohlf (1969) and Siegel & Castellan (1988). Because the assumption of normality of data was not always met and some measured variables represented ordinal data, we used the nonparametric Mann–Whitney ranks test (statistic: z for samples > 20), Kruskal–Wallis 1-way analysis of variance (statistic: H), and the Schreirer–Ray–Hare test (statistic: SH). Multiple comparisons tests were used to examine differences among treatments and among conditions and control trials. G-test adjusted by William's correction was used for frequency data. P values of < 0.05 were considered statistically significant.

RESULTS

Agonistic level within the analysed population

No significant differences were found for any of the variables recorded during the first experimental session. That is, the number of interactions ($H_3 = 1.797$), the average score ($H_3 = 5.815$), dominance ($H_3 = 7.558$), the latency ($H_3 = 5.527$), and the types of interactions ($G_{12} = 16.146$) did not differ among samples of crabs that during the second experimental session were subject to the three treatments and to the control trials. Therefore, the samples we used were subsets of the same population.

Responses to an empty shell in the presence of cues from a conspecific

When treatments and control trials were compared for hierarchical ranks using a two-factor analysis (ranks *vs* conditions), crabs displayed no significantly different responses towards the offered shell in all the recorded variables in relation to their and to their opponent's status (SH_3 between 0.001 and 3.503) and the interaction between hierarchical ranks and conditions was never significant (SH_3 between 0.001 and 1.763). Similar results were obtained by comparing the frequency distributions of the four types of contact with the shell (G_3 between 0.017 and 6.828). Because of this uniformity of behaviour between alphas and betas, data from the two hierarchical ranks were pooled in the following analyses.

The Mann–Whitney ranks test and the Schreirer–Ray–Hare test were used, respectively, to compare conditions in each treatment and to perform a two-factorial analysis, the two factors being treatments and conditions (Fig. 1 and Table 1). Crabs approached the shell at the

Table 1. Comparison for the four analysed variables among treatments and between conditions (FC, familiar conspecifics; UC, unfamiliar conspecifics) after a Schreirer–Ray–Hare test (*SH*). Degrees of freedom = 3

	Approach to the shell		Latency		Duration of contacts		Duration of movement	
	SH	*P*	*SH*	*P*	*SH*	*P*	*SH*	*P*
FC *vs* UC	11.372	< 0.001	16.066	< 0.001	27.255	< 0.001	2.117	NS
Among treatments	8.374	< 0.02	12.021	< 0.001	4.408	NS	1.734	NS
Interaction	5.390	NS	7.581	< 0.05	14.487	< 0.001	2.512	NS

Table 2. Comparison for the four analysed variables and types of interactions among treatments distinguished into two conditions (familiar conspecifics, FC, and unfamiliar conspecifics, UC) and the corresponding control trial (with a transparent sector, TR, and with an opaque sector, OP). The statistical test used was the Kruskal–Wallis one-way analysis of variance (H, degrees of freedom = 2), followed by a multiple comparisons test to examine differences between treatments and therefore to construct a hierarchy

	Approach to the shell			Latency		
	H	*P*	Hierarchy	*H*	*P*	Hierarchy
Sight only *vs* TR	1.725	NS	FC = UC = TR	0.321	NS	FC = UC = TR
Smell only *vs* OP	8.528	< 0.02	FC = UC < OP	14.269	< 0.001	OP = UC < FC
Sight and smell *vs* TR	24.344	< 0.001	FC = UC < TR	24.603	< 0.001	UC = TR < FC
	Duration of contacts			Duration of movement		
	H	*P*	Hierarchy	*H*	*P*	Hierarchy
Sight only *vs* TR	0.221	NS	FC = UC = TR	3.925	NS	FC = UC = TR
Smell only *vs* OP	21.308	< 0.001	FC < OP = UC	3.496	NS	FC = UC = OP
Sight and smell *vs* TR	25.719	< 0.001	FC < UC = TR	8.617	< 0.02	FC = UC < TR

contemporaneous sight and smell of the conspecific less frequently than at its only sight or smell; only in the 'sight and smell' treatment, the number of approaches to the shell was significantly higher in UC than in FC conditions ($z = 3.844$, $P < 0.001$). As shown by analysing latency, crabs were less reactive towards the shell when they simultaneously viewed and smelled a conspecific than at its sight only or smell only; latency was longer in FC than in UC conditions in both 'smell only' ($z = 3.017$, $P < 0.001$) and 'sight and smell' ($z = 3.801$, $P < 0.001$) treatments. Overall, contacts with the shell had the same duration in the three treatments; crabs significantly interacted with the shell for a longer time in the UC condition for both the 'smell only' ($z = 4.258$, $P < 0.001$) and the 'sight and smell' ($z = 4.330$, $P < 0.001$) treatments, but not for the 'sight only' treatment. Movement did not differ among treatments or between conditions, and there was no significant interaction. No difference was found for any of the four analysed variables when the two control trials were compared ($z < 1.212$).

In the 'smell only' and in the 'sight and smell' treatments (but not in both the 'sight only' treatment and in the control trials where G_3 was 1.109 and 6.828, NS), the types of contacts with the shell had different frequency distributions between the two conditions ($G_3 = 42.280$ and 12.352, $P < 0.01$), shells being more often avoided in FC and more often explored in UC conditions.

Comparison between treatments and control

Each treatment was compared with the corresponding control trial using the Kruskal–Wallis one-way analysis of variance (i.e. 'sight only' and 'sight and smell' treatments with the TR control trial; 'smell only' treatment with the OP control trial; Fig. 1) followed by a multiple comparisons test to examine eventual differences between treatments. While responses towards an empty shell did not differ between the 'sight only' treatment and the TR control trial, a difference was noted when the comparison among conditions was made within the two other treatments (Table 2). In particular, behaviour differed between the FC condition and the control trials (either OP or TR) in three (in the 'smell only' treatment) and in all (in the 'sight and smell' treatment) of the four recorded variables ($P < 0.05$).

DISCUSSION

Many activities in aquatic invertebrates are known to be affected by external chemicals, including gregarious settlement and metamorphosis of invertebrate larvae (e.g. Rittschof, 1985), larval release by crustacean decapods (e.g. Forward, Rittschof & DeVries, 1987), identification of brooding females by crayfish larvae (Little, 1975), location of empty gastropod shells by hermit crabs (e.g.

McClean, 1974; Rittschof, 1980; Rittschof *et al.*, 1992), alarm responses in gastropods and crayfish (e.g. Atema & Burd, 1976; Hazlett, 1994), localization of food by several organisms (e.g. Bardach, 1975) and prey by snails (Rittschof, Shepherd & Williams, 1984), initiation and maintenance of symbiotic relationships (e.g. Derby & Atema, 1980), signalling of status in lobsters and crayfish (e.g. Karavanich & Atema, 1998; Zulandt Schneider *et al.*, 2001), recognition of self in crayfish (Hazlett, 1985), and mate attraction in both male and female crustaceans (e.g. Dunham, 1978; Bushmann & Atema, 2000).

By analysing *P. longicarpus*' behaviour in response to an empty shell, we showed that this species discriminates between familiar and unfamiliar individuals and that this discrimination is independent of the relative size of the conspecific, as previously suggested by Gherardi & Tiedemann (2004). In addition, we demonstrated that this process of binary recognition is based on chemical signatures, an ability that this species shares with a few other aquatic invertebrates.

One shortcoming of this laboratory study was that the importance of discriminating individual odours in this species' natural environment was not definitively assessed. At this moment, we can only say that this species' social life is complex enough to warrant a form of recognition. *Pagurus longicarpus* establishes and maintains dominance hierarchies, at least in captivity (Allee & Douglis, 1945; Winston & Jacobson, 1978; Gherardi & Tiedemann, 2004), and aggregations of up to 15 individuals occur in tide pools (Scully, 1978) and seem to persist in the same site for several days (pers. obs.).

We have explored the communicative consequences of combining signal components from visual and olfactory channels. Several authors (Hazlett, 1982; Diaz *et al.*, 1994; Chiussi *et al.*, 2001) have found that hermit crabs make use, in complex ways, of chemical and visual stimuli associated with particular types of shells. The present study showed that crabs also respond to chemical cues of conspecifics, when presented with a shell, but not to visual cues alone, and thus that they were able to recognize the conspecific on a chemical, but not a visual, basis. However, chemical and visual stimuli from one unfamiliar individual, if presented together, elicited more pronounced responses than only smell. In fact, in addition to shorter latencies and longer duration of contacts with the shell as in the 'smell only' treatment, crabs in the 'sight and smell' treatment approached the shell a significantly higher number of times when stimuli were emitted by an unfamiliar (than a familiar) conspecific. Furthermore, without distinguishing between these two conditions, crabs appeared less reactive (lower number of approaches to the shell and longer latencies) in the presence of both the smell and the sight of a conspecific than at its smell only or sight only. Olfaction thus appears to be the dominant sensory channel in *P. longicarpus*' binary discrimination, but the potential of its integration with visual stimuli cannot be excluded, supporting the idea that communication is multimodal (Guilford & Dawkins, 1991; Partan & Marler, 1999) also in the context of individual recognition. A potential advantage of multimodality here might be an improvement of the detectability and discriminability (Rowe, 1999) of the identity signals emitted by the receivers.

Chemical detection in this species is a matter of 'nose' and not of 'tongue' (Rittschof & Bonaventura, 1986), since physical contact with the conspecific is not required. *Pagurus longicarpus* was also able to discriminate the odour of a conspecific within a complex olfactory environment that includes the smell emitted by the shells. In addition, crabs reacted differently when exposed to their own odour than to the odour from other individuals (and in particular from a familiar conspecific), suggesting that they do not recognize familiar conspecifics from their own odour left on the opponent's body or shell during previous contacts. Therefore, it seems possible that recognition in this species is more refined than a binary identification, and that chemical 'badges' can be attributes of individual crabs.

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