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ORIGINAL ARTICLE

Francesca Gherardi · John Tiedemann

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Abstract One mechanism that permits the maintenance of dominance hierarchies is individual recognition, defined as the ability of an animal to recognize a conspecific on the basis of one or more identifying cues, and to associate it with experiences of victories or defeats that the animal has gained from preceding encounters with that particular individual. We examined whether the long-clawed hermit crab, *Pagurus longicarpus*, could differentiate between unfamiliar and familiar opponents. The experimental protocol was designed to control in pairs of interacting individuals several factors together, such as status and relative size of the opponent, as well as species, quality, and fit of the inhabited shell. The hermit crabs were more reactive and their agonistic level was higher in unfamiliar than in familiar pairs; in addition, betas were more prone to initiate an interaction with unfamiliar than with familiar alphas. The alternative explanation—that the ability to discriminate between familiar and novel shells can explain our results per se—was tested following, in part, Jackson and Elwood's (1989) protocol for *Pagurus bernhardus* and was, at least for this species, rejected. This study did not determine whether a true individual recognition occurs, but demonstrated that *P. longicarpus* categorizes the individuals into two "heterogeneous subgroups", thus being capable of a binary discrimination among opponents.

Keywords Individual recognition · Dominance hierarchies · Hermit crabs · *Pagurus longicarpus*

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F. Gherardi (✉)
Dipartimento di Biologia Animale e Genetica,
University of Florence, Via Romana 17, I50125 Florence, Italy
e-mail: gherardi@dbag.unifi.it
Tel.: +39-055-2288216
Fax: +39-055-222565

J. Tiedemann
School of Science, Technology and Engineering,
Monmouth University, West Long Branch, N.J., USA

Introduction

A key element for the social organization in many animal taxa is the ability of individuals to recognize each other: social recognition facilitates, or is a prerequisite for, the structure and stability of a number of behavioral networks between individuals, such as dominance hierarchies, territorial defense, competitive aggression, pair bonds, mate selection, and kin favoritism (reviewed in Zayan 1994).

The existence of complex systems of recognition in vertebrates has been consolidated by a plethora of studies (reviewed in Halpin 1980 and, among others, Breed and Bekoff 1981; Colgan 1983; Ydenberg et al. 1988; Zayan 1994). In invertebrates, individual "signature" systems (Beecher 1982) and recognition mechanisms were found almost exclusively within sexual partners (in shrimp *Hymenocera picta*, Seibt and Wickler 1979, *Stenopus hispidus*, Johnson 1977, *Lysmata debelius*, Rufino and Jones 2001, *Alpheus heterochelis*, Rahman et al. 2001; in stomatopods *Gonodactylus bredini*, Caldwell 1992; and in isopods *Hemilepistus reaumuri*, Linsenmair 1985), nestmates (in bees: Bell 1974; in wasps: Tibbetts 2002), and family groups (in isopods *Hemilepistus reaumuri*, Linsenmair 1972, 1985 and *Porcellio* sp., Linsenmair 1984, and in the primitive cockroach, *Cryptocercus punctulatus*, Seelinger and Seelinger 1983).

In members of a rank order, the reduction with time of the frequency and intensity of agonistic contests, resulting from the formation of a dominance hierarchy and the expression of a "social inertia" (Guhl 1968), has been imputed to three possible mechanisms. The first mechanism assumes that in a "confidence" hierarchy (Barnard and Burk 1979), a change in one individual's internal state as an effect of repeated defeats can explain the reduction of the subordinate's aggression (shown, e.g., in the cuttlefish *Sepia officinalis*, Boal 1996). Second, hierarchies (defined in this case as "assessment" hierarchies, Barnard and Burk 1979) may be kept stable through the recognition of the opponent's dominance status by some cue, possibly a pheromone, a posture or a behavior

displayed by the dominant and/or the subordinate that is under the control of one individual's internal state. This mechanism, which does not require prior experience with that particular individual, has been assumed to rule the dominance structure of several invertebrates, including crickets (Alexander 1961), hermit crabs (Winston and Jacobson 1978), and crayfish (Copp 1986; Zulandt Schneider et al. 2001).

The third possibility for hierarchy maintenance is individual recognition, here defined as the ability of an animal to recognize a conspecific individual on the basis of one or more identifying cues, and to associate it with experiences of victories or defeats that the animal has gained from preceding encounters with that particular individual. To our knowledge, only six studies suggest the potential of invertebrates to use individual recognition in the agonistic context, although some appear equivocal (i.e. Lowe 1956 in the crayfish *Cambarellus shufeldtii*; Hazlett 1969 in the hermit crab *Pagurus bernhardus*; Vannini and Gherardi 1981 in the river crab *Potamon fluviatile*; Caldwell 1979, 1985 in the mantis shrimp *Gonodactylus festae*, and Karavanich and Atema 1998 in the lobster *Homarus americanus*).

The long-clawed hermit crab, *Pagurus longicarpus* Say 1817, is common in shallow waters along the western Atlantic coasts of North America, from Nova Scotia south to eastern Florida, and the northern Gulf of Mexico from the west coast of Florida to Texas (Williams 1984). The question here is whether this species can recognize individuals that it has previously encountered (familiar individuals), a capability that can be revealed by the different behavior that hermit crabs display towards unfamiliar and familiar conspecifics within pairs of interacting opponents. If a hermit crab is able to assess its opponent on the basis of signature cues conveyed by the latter as an individual (and not as a representative of a status), and does not alter its behavior simply in response to the estimate of its own competitive ability, we would predict that agonistic level will be higher when faced with unfamiliar than with familiar opponents, and that hermit crabs' behavior will be independent of their own status and the status of the opponent. An alternative explanation is that hermit crabs are able to discriminate between familiar and novel shells, even if seemingly identical, by remembering certain features of already investigated shells, as shown in *Pagurus bernhardus* by Jackson and Elwood (1989).

Previous laboratory studies have demonstrated that this species' social life is complex enough to warrant a form of recognition, thus justifying the above question. In fact, *P. longicarpus* establishes and maintains dominance hierarchies, as shown in groups of at least four individuals kept in captivity (Allee and Douglis 1945; Winston and Jacobson 1978). Moreover, field observations suggested that repeated contacts among a relatively small number of animals may occur, conditions that are necessary for individual recognition. In fact, small aggregations were found in tide pools (Scully 1978), mostly around gastropod predation sites (Rittschof 1980), and persisted in the same place for a relatively short period, between a few hours and two days (personal observation).

Methods

Around 100 hermit crabs with a shield length of 4–6 mm were hand-collected haphazardly from muddy/sandy areas of the Sandy Hook peninsula (New Jersey, USA) in July 2002 during diurnal low tides. At capture, they were kept separated in small groups. In the laboratory, the specimens were maintained in groups of up to 25 individuals for no more than two weeks until used in a temperature-controlled room (22 °C) and under a 14L:10D lighting condition. They were kept in four separate 20-l holding aquaria containing constantly aerated, artificial seawater (Instant Ocean salts) at the same salinity as natural seawater (27 ppt), and fed a diet of commercial shrimp pellets every three days. Water was changed weekly.

To avoid any effect of shell species, size, quality, and fit on *P. longicarpus*' recognition ability, two days before the experiment hermit crabs were given a choice of shells from a number (five per hermit crab) 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 color as uniform as possible. These were prepared by collecting live *I. obsoleta* (the dominant shell species used by the study population), boiling and removing the flesh, rinsing in seawater, and air-drying. Hermit crabs were induced to occupy a new shell by gently breaking with a vice the apex of the shell they inhabited at the time of collection. They 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.

We formed 40 pairs by taking randomly one individual with no missing limbs from each separate holding aquarium to ensure they had no prior knowledge of one another. To reduce any influence of size on dominance and eventual recognition ability, hermit crabs were size-matched by sight, using the major chela length as an index of body size. Measurements taken at the end of the experiment showed that shield lengths of the individuals of a pair differed by less than 4% on average. Sex was not noted since sex has been shown to exert no effect on agonistic interactions in this and other hermit crab species (Hazlett 1966; Winston and Jacobson 1978), at least during non-reproductive periods (in this area, this species reproduces between October and May with a peak in autumn; Wilber 1989). The shells inhabited by the hermit crabs were marked by one or two dots of permanent black ink, while the hermit crabs were recognized by the length of their antennae and by slight differences in cheliped and pereopod color. Pairs were kept in glass bowls (10 cm diameter) containing 160 cc artificial seawater (27 ppt salinity, 22 °C temperature). These were visually isolated from each other and maintained with uniformly colored (white) substrate and background. During observations, glass bowls were illuminated by one 75-W overhead incandescent light, 50 cm over the water level.

The experiment was divided into two subsequent phases: (1) the familiarization phase, and (2) the experimental phase. In the familiarization phase, 40 pairs were kept in the same bowl for two consecutive days. During this period, relationships of dominance and subordinance were established within each pair and revealed after 15 min of observation at the end of the first day of cohabitation. Based on Winston and Jacobson's (1978) data, one day was sufficient for the formation of a dominance hierarchy in this species. However, 30 min before the experimental phase, we checked for the status of each individual (that did not change in any pair) and recorded those shell switches that had eventually occurred overnight (in five pairs).

In the experimental phase, conducted after the second day of cohabitation, each pair was randomly assigned to one of two treatments and then observed for 15 min. Twenty pairs (hereafter called H1 pairs) were subject to a switch of the opponents having the same status, thus obtaining pairs whose individual identity was

unknown but whose status was known to the combatants (unfamiliar opponents, UO, pairs). We were careful to match individuals for size, shield lengths differing between opponents by around 3%. The other 20 pairs (hereafter called H2 pairs) were subject to a sham switch (the control); in these pairs, both the identity and the status of the opponents were known to the combatants (familiar opponents, FO, pairs). The order of the two treatments was determined with a random-numbers table.

In both phases, observations were performed between 0900 and 1600 hours. Immediately preceding the observation of every pair, hermit crabs were removed from their bowl, and after a few seconds were introduced into a novel bowl containing clean seawater and put on the opposite sides of a removable opaque-plastic divider. After 5 min of acclimation, the divider was lifted and the hermit crabs were allowed to interact with each other.

The events occurring during 15 min of observation were described on a tape recorder and, from these records, the following measures for each pair were obtained:

1. Number of interactions. One interaction started when one opponent approached the other and ended when one opponent retreated at a distance longer than 3 cm.
2. Type of interactions. Interactions were distinguished as: avoidance (i.e. one opponent retreated with no overt response by the other); threat (i.e. one opponent retreated when the other extended its chelipeds or raised its pereopods or flicked its antennae or chelipeds—when partly withdrawn into the shell); contact (i.e. one opponent retreated after the occurrence of at least one contact behavior, such as antennal contact, grasp or strike); exploration (i.e. one opponent retreated when the other grasped the other's shell with its chelipeds or pereopods, and/or explored the external features of the shell or its aperture and/or rocked it back and forth); and shell fight (i.e. one opponent retreated after the other had executed at least one bout of shell rapping and, eventually, had evicted it from the shell and had changed to its shell). For the classification of hermit crabs' activities, we followed in part the ethogram provided by Elwood and Glass (1981).
3. Average score. Each type of interactions was ranked on a scale of intensity from 1 to 5. For every 15-min observation, the sum of the scores of each interaction was calculated and divided by the number of interactions to obtain the average score.
4. Latency time, i.e. the time passed between the start of our observation after the divider was lifted and the first approach by one opponent. When no interaction occurred, we arbitrarily assigned a latency time equal to 905 s.
5. Duration of every type of interactions.
6. Overall time spent in interactions (i.e. time in interactions).
7. The initiator of each interaction.
8. The winner (i.e. the opponent that did not retreat from the other or that retreated after the other had withdrawn into the shell).
9. Percentage of dominance, i.e. the number of interactions won by the alpha (i.e. the individual that was the winner of more than 50% of interactions) on the overall number of interactions in percentage. Interactions without a clear winner were excluded from the analysis.

To test whether *P. longicarpus* is able to discriminate between familiar and unfamiliar shells, we carried out an experiment during July 2003 in Woods Hole (Massachusetts, USA) that followed in part Jackson and Elwood's (1989) protocol for *Pagurus bernhardus*. To be consistent with the individual recognition experiment, we tested hermit crabs that inhabited shells of the preferred size, instead of individuals forced to inhabit shells of half the preferred size, as done by Jackson and Elwood (1989). Twenty hermit crabs were collected in Sipperwissett salt marsh, and in the laboratory were subject to a free-access experiment, as described above, that lasted 48 h. Then, hermit crabs were familiarized singularly with an empty periwinkle (*Littorina littorea*) shell in a glass bowl (10 cm diameter). Periwinkle shells were almost exclusively used by *P. longicarpus* in this area. After one day of familiarization, each hermit crab was placed in a similar bowl in the presence of the familiar shell, together with a novel shell of the same species, size, color pattern, and quality, positioned aperture downwards about 6 cm apart, the hermit crab being introduced at an equal distance from both at the opposite side of the bowl. The apertures of the two shells had been blocked with a resin to avoid their occupation by the hermit crab and their relative location in the bowl was inverted between trials. During 5 min of observation, we recorded the first shell explored by the hermit crab, as well as the frequency and duration of its contacts with both shells.

Statistical analyses were performed, following the procedures found in Sokal and Rohlf (1969) and Siegel (1956). Because the assumptions of normality of data and homogeneity of variance were not always met and some measures taken represented ordinal data, we applied nonparametric tests. The Mann-Whitney test (statistic: U, or z when $n>20$) and Schreirer-Ray-Hare test (statistic: H) were used to examine differences between independent samples (H1 vs H2 pairs and UO vs FO pairs), while related samples, i.e. H2 vs FO (in which the same pairs were observed before and after the sham switch of the opponent) and activities towards familiar and unfamiliar shells were analyzed by the Wilcoxon matched-pairs signed-ranks test (statistic: T). G-tests adjusted by William's correction (statistic: G) was used for frequency data. Following Siegel's (1956) recommendation (p 25), text and figures provide medians and 95% errors, which are the statistics most appropriate for describing the central tendency of scores in the ordinal scales analyzed by nonparametric tests. P-values of less than 0.05 were considered statistically significant.

Results

Hermit crabs appeared to be more reactive when they were presented with an unfamiliar individual (i.e. latency time was shorter in UO than in FO pairs, Fig. 1A, Table 1), and interacted more often with it than with a familiar hermit crab, at a higher intensity (i.e. the number of interactions and the average score were higher in UO than in FO pairs, Fig. 1B,C, Table 1), and for a longer time (i.e. the time in interactions was longer in UO than in FO pairs, Fig. 1D, Table 1). In contrast, a sham switch of the opponent did not alter the overall behavior of hermit crabs (i.e. no difference was found between H2 and FO pairs for any of the measures taken) (Fig. 1, Table 1). These results were not the effect of a difference in the agonistic level between pairs that were subject to one of the two experimental treatments, since H1 and H2 pairs did not vary in any of the measures taken (Table 1).

Using a two-factorial analysis, we compared first the H1 and H2 pairs, and second, the UO and FO pairs for the frequencies of types of interactions per pair; factors were the five types of interactions we classified in this study and the two pair categories. First, we showed that frequencies did not significantly differ between H1 and H2 pairs (H=3.581, $P>0.05$; among types of interactions: H=43.112, $P<0.001$; interaction between factors: H=1.212, $P>0.1$). Second, the frequency of threats was higher when hermit crabs of the pair were unfamiliar than when familiar (3 and 3.0–8.6 vs 1 and 0.8–4.1); hermit crabs explored more often the shell of an unfamiliar individual (3 and 1.9–4.0 vs 0 and 0.0–1.0), and only in the presence of an unfamiliar rival escalated into shell fights (1 and 0.3–1.4 vs 0) (H=13.541, n=20,20, $P<0.001$; among types of interaction: H=30.068, $P<0.001$; interaction between factors: H=5.209, $P>0.1$). In contrast, the

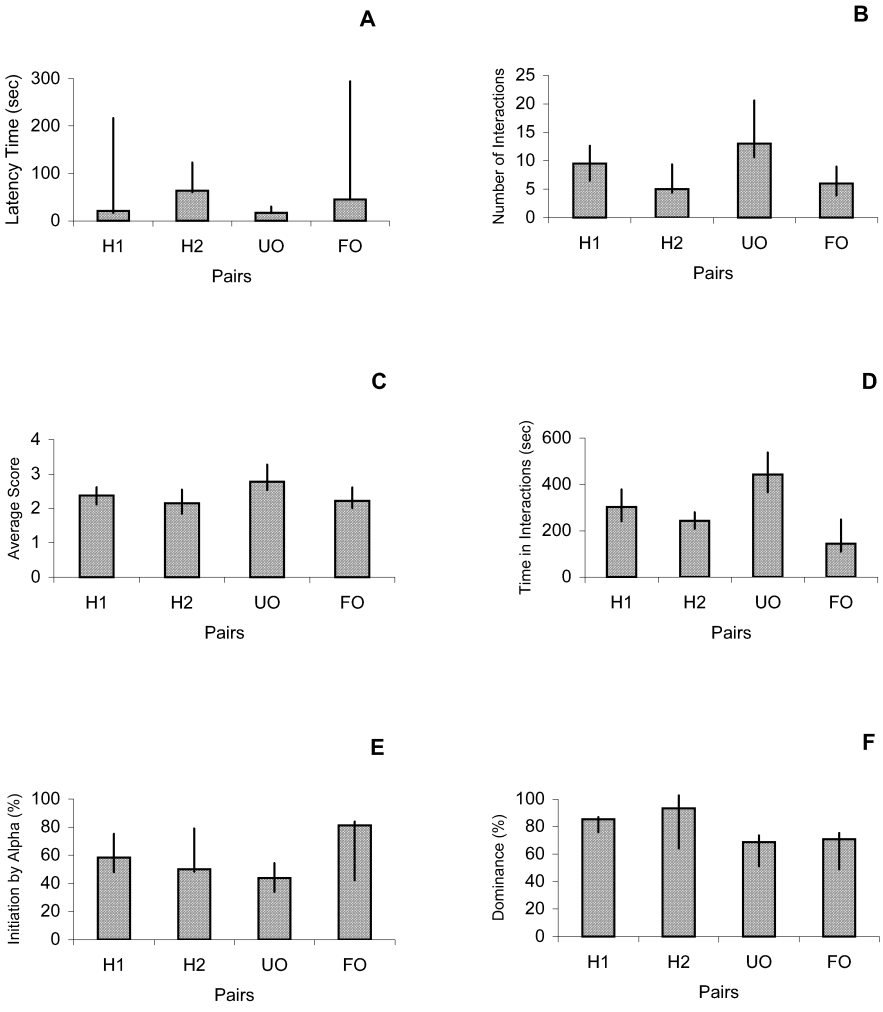

Fig. 1A–F Medians (and 95% error) of Latency Time, Number of Interactions, Average Score, Time in Interactions, Initiation by Alpha, and Dominance, compared among H1, H2, UO, and FO pairs. Sample size was 20 per pair category (exceptions in Table 1). *H1*=pairs of interacting hermit crabs that were subject in the subsequent experimental treatment to a switch of one opponent; *H2*=pairs of interacting hermit crabs that were subject in the subsequent experimental treatment to a sham switch; *UO*=pairs composed of unfamiliar opponents having the same status as the former opponents; *FO*=pairs composed of familiar opponents

Table 1 Latency Time, Number of Interactions, Average Score, Time in Interactions, Initiation by Alpha, and Dominance compared between H1 and H2 pairs, UO and FO pairs, and H2 and FO pairs. Comparisons were made using Mann-Whitney *U*-test (H1 vs H2 and UO vs FO; statistic *U*) and Wilcoxon matched-pairs signed-ranks test for related samples (H2 vs FO; statistic: *T*). H1 and H2 are pairs of the familiarization phase that were subject to, respectively, the subsequent switch and sham switch of the opponent. UO and FO are pairs of the experimental phase composed of, respectively, unfamiliar and familiar opponents

	H1 vs H2			UO vs FO			H2 vs FO		
	U	*P*	*n*	*U*	*P*	*n*	*T*	*P*	*n*
Latency Time (s)	138.5	>0.05	20,20	83	<0.001	20,20	108	>0.05	20
Number of Interactions	152	>0.05	20,20	101	<0.01	20,20	94	>0.05	20
Average Score	141	>0.05	18,20	98.5	<0.01	17,20	68	>0.05	18
Time in Interactions (s)	139	>0.05	20,20	58.5	<0.001	20,20	66	>0.05	20
Initiation by Alpha (%)	167.5	>0.05	18,20	122.5	<0.025	18,20	74	>0.05	18
Dominance (%)	152.5	>0.05	18,18	141.5	>0.05	16,20	43	>0.05	16

occurrence of any type of interaction was not affected by a sham switch, since frequencies did not differ between H2 and FO pairs (avoidance: T=40, n=14; threat: T=62, n=19; contact: T=26, n=14; exploration: T=24, n=13; shell fight: T=0, n=2; P always >0.05).

Excluding shell fights (which occurred only in UO pairs with a duration of 53 and 38–236 s, n=17), we compared UO and FO pairs for the duration of each type of interaction. No difference was found for avoidance (UO: 7 and 7–9 s, n=61; FO: 7 and 7–15 s, n=34; z=0.551, P=0.291), threat (UO: 9 and 9-16 s, n=118; FO: 12 and 12–21 s, n=52; z=0.484, P=0.316), and contact (UO: 19 and 19–34 s, n=56; FO: 32 and 14–84 s, n=26; z=0.872, P=0.192). On the contrary, exploration had a longer duration in pairs composed of familiar (83 and 56–137 s, n=11) than of unfamiliar (40 and 40–62 s, n=57) individuals (z=2.439, P=0.007). Moreover, a comparison between UO and FO pairs for the duration of the first

shell exploration after the switch or the sham switch of the opponent did not show any significant difference (UO: 59 and 45–60 s, n=16; FO: 71 and 58–85 s, n=7; U=39.5, P>0.05).

The different behaviors displayed by hermit crabs when opposed to unfamiliar or familiar individuals were not related to their former status. In fact, in H1, H2, and FO pairs, alphas initiated more than 50% of interactions and no difference was recorded between pairs, while in pairs composed of unfamiliar individuals, the former alpha was the initiator in less than 45% of the interactions (Fig. 1E, Table 1). In UO pairs, individuals that previously were alphas were less likely to win the interactions (however, the observed difference in dominance percentage did not reach significance) (Fig. 1F, Table 1).Then, familiar opponents always maintained the status shown in the preceding day. In contrast, in five UO pairs, former betas became dominant and in four other pairs no clear dominance order was established, at least during the15 min of observation (UO vs FO: G=13.576, df=2, P<0.01).

Pagurus longicarpus did not react differently when presented with familiar and unfamiliar shells. In fact, the first shell investigated was either familiar or unfamiliar (10 vs 10), and the frequency (3 and 2.4–5.8 vs 4 and 2.2–5.0; T=68.5, n=17, P>0.05) and duration (43 and 27–64 s vs 33 and 21–70 s; T=108.5, n=20, P>0.05) of investigation were independent of the hermit crab's familiarity with the shell.

Discussion

A previous study (Winston and Jacobson 1978) had indicated that aggression in hierarchies of *P. longicarpus* is mediated by the recognition of the opponent's "aggressive state" (i.e. the readiness with which an individual engages in agonistic interactions). Our results lead to a different scenario, suggesting that this species is capable of individual recognition. This discrepancy with Winston and Jacobson's (1978) findings may be due to the experimental protocol we followed that allowed us to control several factors together.

Pagurus longicarpus seems to discriminate between individuals on the basis of the experience it has gained in the previous 48 h with the opponent and behaves accordingly, following the simple rule: "If I know the opponent, behave as before; if I do not know it, attack". Thus, agonistic level is higher between unfamiliar than between familiar pairs and betas are more prone to initiate an interaction with unfamiliar than with familiar alphas.

An alternative explanation is that hermit crabs do recognize as familiar the shell inhabited by an opponent that they had previously encountered, being therefore less reactive towards already investigated—and eventually rejected—shells. As a consequence, they may display a lower agonistic level towards familiar individuals, not because they can recognize the hermit crab, but because they discriminate between familiar and novel shells. Indeed, the ability by hermit crabs to remember certain features of shells that they have investigated has been shown in *Pagurus bernhardus* (Jackson and Elwood 1989). The hermit crab sample that we used in our experiments was made as uniform as possible for the inhabited shells, which belonged to the same gastropod species (*I. obsoleta*), had similar relative size and color, and were intact and unfouled. However, Jackson and Elwood (1989) found that hermit crabs display "a remarkably high discriminative ability" (p 533), being capable of distinguishing between two seemingly identical shells. In designing our experiment, we avoided subjecting hermit crabs to any manipulation immediately before the switch (or the sham switch) of the opponent, since this might affect their subsequent behavior; therefore, we had no means of isolating the effect of individual recognition on crab behavior from the eventual effect of shell recognition by, for instance, forcing hermit crabs to enter a novel shell before the experimental treatment. Instead, to falsify the "shell recognition hypothesis" in *P. longicarpus*, we carried out an experiment similar to Jackson and Elwood's (1989) experiment: hermit crabs occupying shells of a preferred size were presented with a familiar shell, together with a novel shell of the same species, size, color pattern, and quality. Our results show that *P. longicarpus*' familiarity with the shell did not affect the frequency and duration of shell investigation and the first shell explored.

Also, from Jackson and Elwood's (1989) results, it is apparent that *P. bernhardus*' shell recognition relies upon stimuli that are perceived by hermit crabs when they are in physical contact with the shell (in fact, the time spent in investigating familiar shells was lower, but the number of approaches to the offered shells was independent of their novelty), while the ability to recognize shells from a distance appeared unfeasible. Similarly, in *P. longicarpus*, the familiarity of a conspecific was perceived at a distance and not when the two hermit crabs were in contact (in fact, both the number of approaches and the latency time differed significantly between UO and FO pairs). However, hermit crabs spent more time interacting with an unfamiliar than with a familiar rival and explored the opponent's shell more often in unfamiliar than in familiar pairs, both results being consistent with the "shell recognition hypothesis". Against this hypothesis, however, we found that: (1) shell explorations, although being more frequent in unfamiliar pairs, lasted for a shorter time in the presence of unknown than of known individuals; (2) the duration of the first shell exploration occurring immediately after the switch or the sham switch of the opponent did not depend on the familiarity with the rival; (3) threats, and not only explorations, occurred more often in the unfamiliar than in the familiar context. Therefore, summing up this information, we exclude the idea that the "shell recognition hypothesis" can provide the only explanation for our results; on the contrary, we must still invoke a form of individual recognition to understand differences in the general behavior displayed by *P. longicarpus* towards unknown and known rivals.

The ability to recognize individuals was shown to be independent of the opponent's status: in unfamiliar pairs, each hermit crab was confronted with an opponent having the same status—and thus a similar "aggressive state"—as the known rival. Besides the hierarchical rank of the opponents and the quality of the inhabited shell, we controlled other features that would possibly influence recognition, such as the relative size of the pair (practically the same), and the environment where pairs were kept and tested (always uniform and novel for all the hermit crabs analyzed). Then, hermit crabs shared the same motivation to interact with the opponent (either unfamiliar or familiar), because each of them inhabited a presumably well-fitting shell resulting from previous free choice among an array of different, undamaged, and unfouled shells. The subpopulation, which the individuals subject to the experimental switch were selected from, showed the same average agonistic level of the subpopulation used for the control treatment.

An obvious shortcoming of our experimental protocol is that it did not allow us to determine whether the species can discriminate one individual of a group from every other individual on the basis of "a unique set of cues defining that individual" (Beecher 1989), showing a "true individual recognition". However, the results of our experiment do demonstrate that *P. longicarpus* categorizes the individuals it encounters into two "heterogeneous subgroups" (Barrows et al. 1975), i.e. the familiar and unfamiliar subgroups, and is thus capable of a binary discrimination among opponents (Archawaranon et al. 1991; Boal 1996). However, as pointed out by Barnard and Burk (1979), the distinction between true individual recognition and other 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.

Further researches are clearly needed to understand the adaptive significance of individual discrimination in the natural environment of *P. longicarpus* and within its biological constraints. Other studies are in progress to better define in this species the "assessment unit" (i.e. the array of cues used by this hermit crab in recognizing the opponent, Barnard and Burk 1979) which, although limited by both energetic costs and its physiology, must be complex enough to make the assessment mechanism uncheatable.

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