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Memory of Social Partners in Hermit Crab Dominance

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Abstract

We investigated the possibility that invertebrates recognize conspecific individuals by studying dominance relationships in the long-clawed hermit crab, *Pagurus longicarpus*. We conducted three sets of laboratory experiments to define the time limits for acquiring and maintaining memory of an individual opponent. The results reveal two characteristics that make individual recognition in this species different from standard associative learning tasks. Firstly, crabs do not require training over many repeated trials; rather, they show evidence of recognition after a single 30-min exposure to a stimulus animal. Secondly, memory lasts for up to 4 d of isolation without reinforcement. A third interesting feature of individual recognition in this species is that familiar opponents are recognized even before the formation of a stable hierarchical rank. That is, recognition seems to be relatively independent of repeated wins (rewards) or losses (punishments) in a dominance hierarchy. The experimental protocol allowed us to show that this species is able to classify conspecifics into two 'heterogeneous subgroups', i.e. familiar vs. unfamiliar individuals, but not to discriminate one individual of a group from every other conspecific from 'a unique set of cues defining that individual'. In other words, we demonstrated a 'binary' – and not a 'true' – individual recognition. However, 1 d of interactions with different crabs did not erase the memory of a former rival, suggesting that *P. longicarpus* uses a system of social partner discrimination more refined than previously shown.

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Introduction

The ability to recognize individuals is essential to several aspects of social behavior, such as the maintenance of stable social groups, parent-offspring or mate relationships, inbreeding avoidance, and the modulation of competitive

relationships. The complexity of the social life in several non-eusocial invertebrates should warrant the evolution of sophisticated forms of recognition. Most cases of individual recognition in invertebrates have been found in arthropods and almost exclusively within sexual partners (isopods – *Hemilepistus reaumuri*, Linsenmair 1985; shrimp – *Stenopus hispidus*, Johnson 1977; *Hymenocera picta*, Seibt & Wickler 1979; *Lysmata debelius*, *Alpheus heterochelis*, Rahman et al. 2001; Rufino & Jones 2001; stomatopods – *Gonodactylus bredini*, Caldwell 1992), nestmates (bees: Bell 1974; wasps: Tibbetts 2002), or family groups (cockroach *Cryptocercus punctulatus*, Seelinger & Seelinger 1983; isopods – *H. reaumuri*, Linsenmair 1972, 1985; *Porcellio* sp. Linsenmair 1984). There are only few examples of invertebrate species that use individual recognition to maintain stable dominance hierarchies (i.e. crayfish *Cambarellus shufeldtii*, Lowe 1956; hermit crab *Pagurus bernhardus*, Hazlett 1969; mantis shrimp *G. festae*, Caldwell 1979, 1985; river crab *Potamon fluviatile*, Vannini & Gherardi 1981; lobster *Homarus americanus*, Karavanich & Atema 1998).

Three alternative mechanisms have been invoked to explain the formation and the maintenance of a rank order. First, an individual can estimate its competitive ability from previous wins and losses, thus establishing its level of 'confidence' (Barnard & Burk 1979). Confidence reflects the animal's expectation of the outcome of future fights, regardless of the opponent, and can be seen in its motivation to attack (e.g. cuttlefish *Sepia officinalis*, Boal 1996). The second mechanism is status recognition with the establishment of 'assessment' hierarchies (Barnard & Burk 1979), in which the agonistic potential of an individual can be assessed from a signal (for instance a pheromone) that provides information on an animal's physical ability or fighting experience (e.g. crayfish, Zulandt Schneider et al. 2001; Gherardi & Daniels 2003; crickets, Alexander 1961).

Finally, hierarchies can be maintained through individual recognition, i.e. the ability of an animal to discriminate one individual of a group from every other conspecific from 'a unique set of cues defining that individual' (Beecher 1989). From this definition, individual recognition seems to be a relatively complex task for invertebrates. However, Barnard & Burk (1979) pointed out that recognition acts 'on a continuous scale of cue complexity ranging from simple cues to complexes possibly beyond the level of the individual' (p. 66). This blurs the distinction between 'true' individual recognition and other apparently simpler forms of individual discrimination.

So far, research on individual recognition in invertebrates has compared responses of animals to two (or three, Caldwell 1985) categories of opponents, which demonstrates an animal's ability to classify conspecifics into two (or three) 'heterogeneous subgroups' (e.g. familiar vs. unfamiliar individuals, Barrows et al. 1975) as the result of a 'binary' (or a 'ternary') individual discrimination (Boal 1996).

The long-clawed hermit crab, *P. longicarpus* Say 1817, is common in shallow waters along the western Atlantic coasts of North America, from Nova Scotia to eastern Florida, and in the northern Gulf of Mexico from the west coast of Florida to Texas (Williams 1984). Since Allee & Douglis (1945), we know that this species establishes dominance hierarchies, at least in a group of four individuals in

captivity. Premises of the present study are Gherardi & Tiedemann's (2004a, b) findings that: (1) hierarchies in *P. longicarpus* are maintained stable with time through a form of binary recognition between familiar and unfamiliar conspecifics (and not by the recognition of the opponent's 'aggressive state'; Winston & Jacobson 1978), (2) this is not a consequence of recognizing the familiar/novel shells the opponents inhabit (contrary to *P. bernhardus*; Jackson & Elwood 1989), and (3) binary individual recognition in this species is mediated by chemical cues.

We used the following rationale for our experimental procedure. If hermit crabs assess conspecifics as individuals, fights between familiar opponents should be shorter and/or less intense than fights between unfamiliar opponents (Karavanich & Atema 1998). Further, subordinates should be less likely to initiate a fight with dominant individuals. If they behaved exclusively in accordance with their own 'confidence', fight duration/intensity and fight initiation should be independent of prior individual knowledge and should rather depend on the confidence of the opponent. If crabs recognized the opponent by status/rank in relation to their own rank, then they should adjust their fight intensity and probability of initiation, again regardless of prior familiarity.

Based on this reasoning, we attempted to answer three questions to elucidate some features of binary individual recognition in *P. longicarpus*:

1. What is the minimum time required by a crab to learn the opponent as a familiar individual?

2. How long does the memory of the opponent last when individuals have been kept in isolation?

3. Is the memory of the original opponent affected by interactions with a group of other conspecifics?

Methods

Subjects, Collection and Housing Conditions

Between Jul. and Aug. 2003, around 300 hermit crabs with a shield length of 4–6 mm were hand-collected haphazardly from Little Sippewissett salt marsh (Falmouth, MA, USA) during diurnal low tides. Immediately after capture, the crabs were separated into small groups; in the Marine Biological Laboratory at Woods Hole, they were maintained in groups of up to 25 individuals for no more than 2 wk until used. The groups were kept in a temperature controlled room (22 °C) and under a natural 14L:10D cycle in separate 20-l holding aquaria containing constantly aerated seawater. They were fed a diet of commercial shrimp pellets every third day. Water was changed weekly. After being used in experiments, crabs were released at the collection site.

Preliminary Free-choice Experiment

To avoid effects of shell properties (species, size, quality, and fit) on *P. longicarpus*' behavior and to equalize its motivation for obtaining a new shell,

crabs were given a choice of five empty, unfouled, and undamaged shells of different size (10–25 mm for base–apex axis) with a color as uniform as possible (following Angel 2000). These were prepared by collecting live periwinkle *Littorina littorea* (the dominant shell type used by the study population), boiling them and removing the flesh. Afterwards, shells were rinsed in seawater and air-dried. 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. For all subsequent experiments crabs were assumed to inhabit a shell of adequate size as a result of this free-choice experiment.

General Experimental Protocol

The general protocol for the three experiments was as follows. A total of 124 pairs were formed by randomly selecting individuals with no missing limbs from separate holding aquaria 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 measuring the major chela width with calipers. Measurements taken at the end of the experiment showed that the shield length (i.e. the length of anterior calcified portion of the cephalothorax) of the individuals of a pair differed less than 3% on average (range: 1.8–2.9%). We did not note the sex of individuals as it has been shown to exert no effect on agonistic interactions in this and other hermit crab species (Hazlett 1966; Winston & Jacobson 1978), at least during the non-reproductive period (this species reproduces between Oct. and May with a peak in autumn; Wilber 1989). To permit identification by the observer, the shells of every pair were marked by one or two dots of permanent black ink, while hermit crabs were recognized by the length of their antennae and by slight differences in cheliped and pereopod color.

All experiments were staged in opaque plastic bowls (10 cm diameter) containing 160 cc unfiltered seawater and illuminated during observations by a 75-W overhead incandescent light 50 cm over the water level. Observations were conducted between 09:00 and 16:00 hours for 10 min each. Before every observation, pairs were introduced into the opposite sides of a removable opaque plastic divider and, after 3 min of acclimation, the divider was lifted and the hermit crabs were allowed to interact. The events occurring during 10 min of observation were described on a tape recorder. From these records, for every pair, we measured (details in Gherardi & Tiedemann 2004a):

1. Duration of Interactions. An agonistic interaction began when one opponent approached the other and ended when one of the two crabs retreated at a distance longer than one body length for at least 10 sec. We excluded the instances of 'avoidance' from the analysis (i.e. one opponent retreated with no overt response by the other). In no cases crabs were seen inactive during interactions.

2. Intensity of Interactions. Intensity was measured as the number of 'strong agonistic behaviors' executed by both crabs. Strong agonistic behaviors included grasps (one crab grips the opponent or the opponent's shell using one or both

chelae), strikes (one crab strikes its opponent's body using one, rarely both, chelipeds), bouts of shell rapping (the attacking crab raps its shell against the shell of the defending crab), and evictions (the attacking crab evicts the other from its shell).

We defined as dominant (alpha) the individual that won more than half of the interactions; the other crab was classified as subordinate (beta). We also computed the instances of dominance reversal between consecutive 10-min observations. Those crabs that did not retreat at the end of the interaction or that retreated after the other withdrew into its shell were deemed as winners. We never observed dominance reversal within one 10-min observation. In the few instances in which both crabs won the same number of interactions, we defined the more active animal (i.e. the crab that spent more time exploring the experimental bowl) as alpha. We computed the frequency of the interactions initiated by betas as an index of their motivation to interact (possibly reflecting their ability of recognizing the rival). One might expect that subordinate crabs recognizing conspecifics as alphas would be less motivated to initiate a fight than when opposed with unknown or unrecognized individuals.

Experiment 1: Learning Time

Pairs were allowed to cohabit (familiarization phase) for 10 or 30 min or 3 h (20 replicates each). At the beginning of their cohabitation, pairs were observed for 10 min (observation 1); at the end of the familiarization phase, they were checked for shell switches and then subjected to the experimental manipulation. Manipulation consisted of separating combatants of every pair and then recombining pairs either with an unfamiliar individual of similar status, size, and shell as the previous opponent (switch) or with the familiar individual itself (sham switch). Therefore, after a switch and a sham switch we obtained, respectively, 10 unfamiliar (UP) and 10 familiar (FP) pairs for each of the three familiarization treatments. Assignment to UP or FP was randomized. Immediately after recombination, pairs were observed for 10 min (observation 2) as before.

Experiment 2: Memory Duration in Isolation

Twenty-four pairs were allowed to cohabit for 2 d during the familiarization phase. Two 10-min observations were done during this phase, after one day of cohabitation (observation 1) and immediately before separating crabs on the second day (observation 2). During the separation phase individuals were kept in isolation for 2, 4 or 6 d (eight replicates each). At the end of this phase, we formed unfamiliar or familiar pairs following the same experimental manipulations as in experiment 1 and we observed all pairs for 10 min (observation 3).

Experiment 3: Memory Duration with Social Contact

The same experimental protocol as expt 2 was followed for a total of 40 pairs, except that the separation phase lasted only 1 d. During the separation phase,

20 hermit crabs were housed each in the presence of five novel conspecifics taken from the holding aquarium, while the other 20 crabs were kept alone. After the 1-d separation, we assigned the animals to UP and FP groups as before, but now each group was made of 10 pairs with social experience and 10 pairs with isolation experience.

Statistical Analyses

Statistical analyses were performed following procedures found in Zar (1984) and in Siegel & Castellan (1988). We applied non-parametric tests, because the assumptions of normality of data and homogeneity of variance were not always met and some data were measured on an ordinal scale. For independent samples we used Mann–Whitney U-tests (statistic: U), Kruskal–Wallis one-way analyses of variance (statistic: H), and Schreirer–Ray–Hare two-factor analyses of variance (statistic: Sr; Schreirer et al. 1976). Related samples were analyzed by Wilcoxon matched-pairs signed-ranks tests (statistic: T) and Friedman two-way analyses of variance (statistic: Fr). When the null hypothesis was rejected after a Friedman two-way analysis of variance, we applied a multiple comparisons test (Siegel & Castellan 1988) to determine which pairs of samples differed significantly (α levels were corrected by Bonferroni adjustment). Fisher exact probability tests or G-tests adjusted by William's correction for $n > 20$ (statistic: G) were used for frequency data. We provide medians and interquartile ranges (first-third quartiles) in text and figures. p-values of less than 0.05 were considered statistically significant.

Results

Familiarization Phase

For every treatment of each experiment, pairs that were subsequently subjected to the different experimental manipulations did not significantly differ for any of the measurements taken (Table 1), suggesting that the samples were drawn from the same population. Only four of 124 (3%) pairs switched their shell during the familiarization phase; this low number of shell switches confirms that the preliminary free-choice experiment provided them with adequate shells and reduced their motivation to switch shells. Dominance reversals between the first and the second day of cohabitation in expts 2 and 3 occurred only in four of 64 pairs (6.25%), showing that 1 d is sufficient for the formation of a stable hierarchy in this species (Winston & Jacobson 1978).

Experiment 1: Learning Time

Familiarity with the opponent reduced both Duration of Interactions ($Sr = 4.918$, $df = 1,36$, $p < 0.05$) and Intensity of Interactions ($Sr = 15.875$, $df = 1,36$, $p < 0.001$), while familiarization time had no effect on any measurement

Table 1: Familiarization phase

	Duration of Interactions			Intensity of Interactions			Beta as Initiator		
	U/H	n,n/n	p-value	U/H	n,n/n	p	U/H	n,n/n	p-value
Expt 1, 10 min	14	6,6	0.294	13.5	6,6	0.268	11	6,6	0.155
Expt 1, 30 min	44.5	10,10	>0.1	48	10,10	>0.1	32.5	10,10	>0.1
Expt 1, 3 h	47	10,10	>0.1	35.5	10,10	>0.1	42.5	10,10	>0.1
Expt 2, obs 1	61	12,12	>0.1	63.5	12,12	>0.1	70	12,12	>0.1
Expt 2, obs 2	44	12,12	>0.1	61	12,12	>0.1	69.5	12,12	>0.1
Expt 3, obs 1	0.383	3	>0.1	4.033	3	>0.1	0.644	3	>0.1
Expt 3, obs 2	1.631	3	>0.1	4.334	3	>0.1	0.472	3	>0.1

Duration of Interactions, Intensity of Interactions, and instances of Beta as Initiator are compared between groups of pairs used to form UP (unfamiliar pairs) and FP (familiar pairs). In expt 1, groups of pairs subjected to a familiarization of 10, 30 min or 3 h were analyzed separately by Mann–Whitney U-tests (statistic: U; n,n, numbers of replicates in the two groups).

The same statistical test was used in expt 2. In expts 2 and 3, comparisons between groups were made in both the first (obs 1) and the second (obs 2) 10-min observations. In expt 3, Kruskal–Wallis one-way analyses of variance (statistic: H; n, sample size) were used to compare the four groups of pairs used to form UP and FP that were kept in isolation or in a group during the separation phase.

(Duration of Interactions: $Sr = 2.138$, $df = 1,36$, $p > 0.05$; Intensity of Interactions: $Sr = 1.293$, $df = 1,36$, $p > 0.1$). The interaction between the two factors (familiarity to the opponent × familiarization time) was not significant (Duration of Interactions: $Sr = 4.354$, $df = 1,36$, $p > 0.1$; Intensity of Interactions: $Sr = 3.813$, $df = 1,36$, $p > 0.1$).

The overall difference between FP and UP was due to the pairs whose familiarization phase lasted for 30 min or 3 h. A familiarization of 10 min was not sufficient to reduce future duration or intensity of interactions (Fig. 1a, b and Table 2). On the contrary, a longer familiarization was followed by a longer duration of interactions in UP than in FP (3 h), with a more frequent recourse to strong agonistic behavior patterns (30 min and 3 h) (Table 2, Fig. 1a, b).

Regardless of the time to familiarize, alphas and betas initiated a similar number of interactions (Fig. 1c and Table 2). However, hierarchies formed after 10 or 30 min of familiarization seemed not to be stable. Dominance reversals were observed in 50% of the cases after 10 and 30 min of familiarization (UP vs. FP, Fisher exact probability test, 10 min: $p = 0.716$; 30 min: $p = 0.188$; Fig. 1d), but ceased entirely after a 3-h familiarization time ($p = 0.016$) (Fig. 1d).

Experiment 2: Memory Duration in Isolation

Duration of Interactions ($Sr = 3.203$, $df = 1,36$, $p > 0.05$) and Intensity of Interactions ($Sr = 2.205$, $df = 1,36$, $p > 0.1$) were independent of the time of

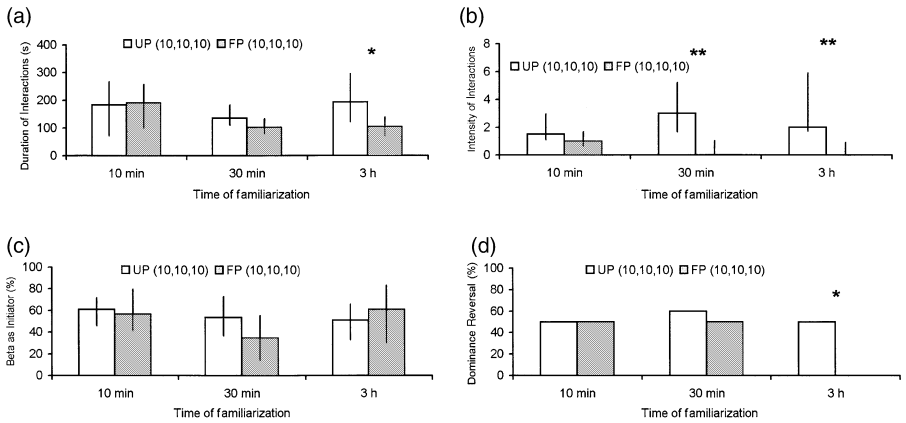

Fig. 1: Median values (and interquartile ranges) of (a) Duration of Interactions, (b) Intensity of Interactions, (c) instances of Beta as Initiator, and (d) frequency (%) of Dominance Reversals, comparing unfamiliar (UP) and familiar (FP) pairs after 10, 30 min, and 3 h of familiarization (expt 1). One and two asterisks mean that UP/FP are different for $p < 0.05$ and $p < 0.01$, respectively (see Table 2 for statistical outputs)

Table 2: Expt 1

	Duration of Interactions			Intensity of Interactions			Beta as Initiator		
	U	n,n	p-value	U	n,n	p-value	U	n,n	p-value
(a) Obs 2: UP vs. FP									
10 min	48	10,10	>0.1	36	10,10	>0.1	50	10,10	>0.1
30 min	33	10,10	>0.05	17.5	10,10	<**0.01**	32.5	10,10	>0.1
3 h	21	10,10	<**0.025**	12	10,10	<**0.01**	42.5	10,10	>0.1
	T	n	p-value	T	n	p-value	T	n	p-value
(b) FP: obs 1 vs. obs 2									
10 min	11	6	>0.1	5	4	>0.1	7.5	6	>0.1
30 min	14	10	>0.1	11	7	>0.1	22	9	>0.1
3 h	23	10	>0.1	9	7	>0.1	27	10	>0.1

In (a), pairs (UP and FP) analyzed in obs 2 are compared using Mann–Whitney U-tests for the three measurements taken.
In (b), obs 1 and obs 2 were compared for FP using Wilcoxon–matched pairs signed-ranks tests (statistic: T; n = number of pairs without ties).
p-values of less than 0.05 are given in bold.

isolation (2, 4 or 6 d). Crabs were more aggressive when opposed with unfamiliar than with familiar conspecifics (Duration of Interactions: $Sr = 4.385$, $df = 1,36$, $p < 0.05$; familiarity to the opponent × time of isolation: $Sr = 0.282$, $df = 1,36$, $p > 0.1$; Intensity of Interactions: $Sr = 4.32$, $df = 1,36$, $p < 0.05$; familiarity to

the opponent × time of isolation: Sr = 3.885, df = 1,36, p > 0.1). This difference was mostly due to the behavior of pairs that had been separated for 2 and 4 d (Fig. 2a, b and Table 3). The interactions occurring in FP after 2, 4, and 6 d of isolation had a similar duration and intensity in the three 10-min observations (Table 3).

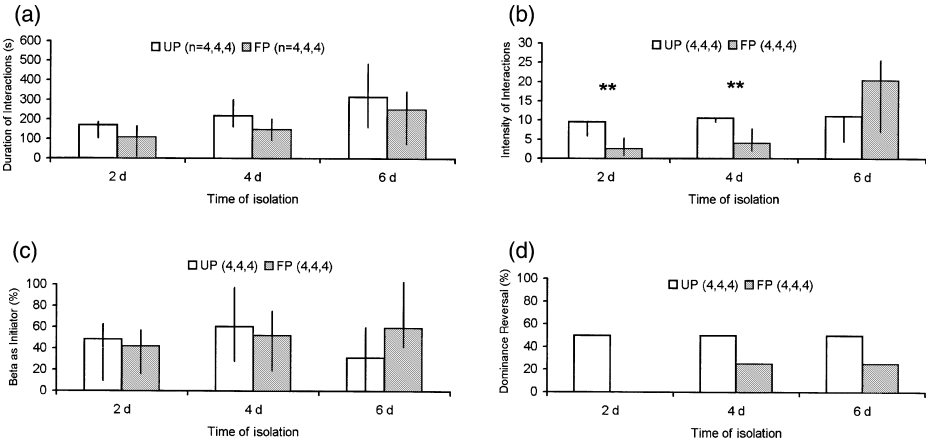

Fig. 2: Comparison of unfamiliar (UP) and familiar (FP) pairs when experimental manipulations were performed after a separation phase of 2, 4, and 6 d in isolation (expt 2; other details in Fig. 1; see Table 3 for statistical outputs). Differences between UP and FP of Dominance Reversals were computed by pooling data from the three conditions

Table 3: Expt 2

	Duration of Interactions			Intensity of Interactions			Beta as Initiator		
	U	n,n	p-value	U	n,n	p-value	U	n,n	p-value
(a) Obs 3: UP vs. FP									
2 d	6	4,4	0.343	1	4,4	**0.029**	7	4,4	0.443
4 d	2	4,4	0.057	0	4,4	**0.014**	5.5	4,4	0.293
6 d	6	4,4	0.343	4	4,4	0.171	7	4,4	0.443
	Fr	k,n	p-value	Fr	k,n	p-value	Fr	k,n	p-value
(b) FP: obs 1 vs. obs 2 vs. obs 3									
2 d	0.5	3,4	0.969	2.923	3,4	0.492	0.933	3,4	0.922
4 d	2	3,4	0.668	4.769	3,4	0.242	0.143	3,4	1
6 d	0.5	3,4	0.969	3.846	3,4	0.342	0.5	3,4	0.969

In (a), pairs (UP and FP) analyzed in obs 3 are compared using Mann–Whitney U-tests. In (b), all the observations for FP are compared using Friedman two-way analyses of variance for related samples (statistic: Fr; k = samples, n = replicates).
p-values of less than 0.05 are given in bold.

Subordinates initiated on average 50% of interactions, without any difference between UP and FP (Fig. 2c and Table 3). However, hierarchies appeared to be stable. Familiar opponents maintained the hierarchical status shown in the preceding observations in 11 (of 12) pairs (Fig. 2d). This was not because of a 'loser effect' (Dugatkin 1997), since in half (6/12) UP former betas became dominant (UP vs. FP, after Fisher exact probability test: $p = 0.034$) (Fig. 2d).

Experiment 3: Memory Duration with Social Contacts

Interactions lasted for a longer time ($Sr = 4.92$, $df = 1,36$, $p < 0.05$) and were more intense ($Sr = 23.58$, $df = 1,36$, $p < 0.001$) in UP than in FP whatever the condition of separation was (Fig. 3a, b and Table 4). However, isolation was followed by combating for a longer time ($Sr = 3.899$, $df = 1,36$, $p < 0.05$; familiarity to the opponent × condition of separation: $Sr = 0.237$, $df = 1,36$, $p > 0.1$) but with the same intensity ($Sr = 2.858$, $df = 1,36$, $p > 0.1$; familiarity to the opponent × condition of separation: $Sr = 0.354$, $df = 1,36$, $p > 0.1$). Isolation seemed to exert an effect also on the intensity of fights in FP (Table 4), but multiple comparisons tests and Bonferroni adjustments did not reveal any significant differences among the three 10-min observations.

Former subordinates were more prone to approach the rival when it was an unfamiliar – rather than a familiar – alpha ($Sr = 4.98$, $df = 1,36$, $p < 0.05$), especially when they had been kept isolated during the separation phase (Fig. 3c and Table 4). Crabs reversed their status in 11 instances of UP out of 20 replicates, but only in two instances of FP (UP vs. FP: $G = 9.495$, $df = 1$, $p < 0.01$) (Fig. 3d).

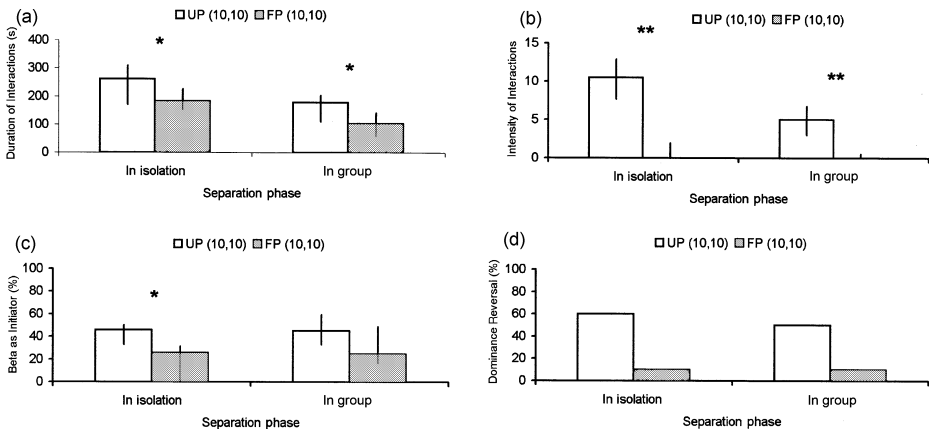

Fig. 3: Comparison of unfamiliar (UP) and familiar (FP) pairs when experimental manipulations were performed after a separation phase of 1 d either in isolation or in a group composed of other five conspecifics (expt 3; other details in Fig. 1; see Table 4 for statistical outputs). Differences between UP and FP of Dominance Reversals were computed by pooling data from the two conditions

Table 4: Expt 3

	Duration of Interactions			Intensity of Interactions			Beta as Initiator		
	U	n,n	p-value	U	n,n	p-value	U	n,n	p-value
(a) Obs 3									
In isolation	27	10,10	< **0.05**	1.5	10,10	< **0.001**	27	10,10	< **0.05**
In a group	21	10,10	< **0.025**	6.5	10,10	< **0.001**	29.5	10,10	> 0.05
	Fr	k,n	p-value	Fr	k,n	p-value	Fr	k,n	p-value
(b) FP: obs 1 vs. obs 2 vs. obs 3									
In isolation	1.647	3,10	> 0.1	8.406	3,10	< **0.05**	5.553	3,10	> 0.05
In a group	2.455	3,10	> 0.1	3.54	3,10	> 0.1	3.744	3,10	> 0.1

In (a), pairs (UP and FP) analyzed in obs 3 are compared using Mann-Whitney U-tests. In (b), FP kept in isolation or in a group during the separation phase are compared using Friedman two-way analyses of variance for related samples (statistic: Fr; k = samples, n = replicates).
p-values of less than 0.05 are given in bold.

Discussion

Our results confirm that *P. longicarpus* is able to remember familiar opponents for a given time, as suggested in a preceding study (Gherardi & Tiedemann 2004a). If a hermit crab has experienced a succession of wins and losses in previous one-on-one encounters, it can follow a simple rule when engaged in a subsequent encounter: 'If you know the opponent, behave as before; if you do not know it, fight longer and stronger'. Consequences would be that, within a given time limit, fights last longer and are more intense, and dominance reversals are more frequent in unfamiliar – rather than in familiar – pairs. Additionally, losers appeared less prone to attack unknown – rather than known – dominants, at least when hierarchies were consolidated (expt 3). Together, these results suggest that recognition of the opponent in this species relies on individual attributes, rather than on dominance status.

However, this evidence from a laboratory study leaves the question unanswered of the adaptive significance of individual recognition. Notwithstanding that *P. longicarpus* has been the subject of several field investigations (e.g. Rebach 1978; Scully 1979; Wilber & Herrnkind 1982, 1984; Pechenik & Lewis 2000), its social behavior in the natural environment is virtually unknown. We can only infer from haphazard observations that repeated contacts among a relatively small number of animals may occur, which is a condition required for individual recognition. 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 2 d (F. Gherardi, pers. obs.).

Our study contributes to the understanding of individual recognition in invertebrates by outlining the process leading hermit crabs to learn social partners. Similarly to the results of Karavanich & Atema (1998) for American lobsters, we found two characteristics that differentiate individual recognition from standard associative learning tasks. Firstly, crabs do not require to be trained over many repeated trials; rather, they show evidence of recognition after a relatively brief exposure to the stimulus animal. The results of expt 1 indicate that a 30-min encounter is sufficient for crabs to learn the opponent's identity (a 20-min fight for lobsters, Karavanich & Atema 1998). Secondly, although memory for individuals can be acquired rapidly, it lasts for a relatively long-time without the need of being constantly exposed to the stimulus. Notwithstanding the obvious limitation of a small sample size, expt 2 shows that a 4-d period of isolation (1–2 wk in lobsters, Karavanich & Atema 1998) is the time limit to remember the conspecific, while after 6 d the memory may have faded. Similarly, in the stomatopod *G. bredini*, Caldwell (1992) demonstrated that the memory of sexual partners lasted for at least 2 wk after the female had spawned and the male had left her cavity. Obviously, further studies are needed to detail the dynamics of social partner learning in hermit crabs as it was done for other types of learning in a few invertebrate models (e.g. Carew & Sahley 1986; Menzel et al. 2001). In particular, it should be necessary to explore the eventual interplay between a short-term memory (created by a single conditioning trial) and a long-term memory (appearing only after multiple conditioning trials) (Kaiser et al. 2003).

We drew our conclusions on the memory of social partners from the analysis of both duration and intensity of agonistic interactions. In expt 1, interactions lasted for a longer time in unfamiliar – rather than in familiar – pairs after 30 min of cohabitation and were more intense after 30 min and 3 h, but not after 10 min; in expt 2, intensity was still higher after isolation of 2 and 4 d, but not of 6 d. It is consistent with these findings that former losers of expt 2 (which initiated 50% of interactions on average) became dominant individuals in half of the unfamiliar pairs, but only in one familiar pair. On the contrary, familiarization in expt 1 seemed to be too short to generate a stable dominance hierarchy. This result suggests a third interesting feature of individual recognition in *P. longicarpus*: its relative independence of dominance. That is, a crab can recognize an opponent without the need of having experienced repeated wins or losses while fighting with it.

Numerous studies have shown that in crustacean decapods social isolation strongly affects aggression (see, e.g. Dunham 1972; Grant & Ulmer 1974). This is in part verified also in this species. After 1 d of isolation, crabs showed the tendency to combat with the former opponent for a longer time than during the familiarization phase (expt 3). However, fights were even longer and more intense in unfamiliar pairs and unfamiliar crabs with a social experience during the separation phase behaved more aggressively than familiar crabs subjected to the same treatment. These two results suggest that the intense fighting recorded after having switched the opponent cannot be attributed solely to the rise of internal aggression with isolation, but it is mostly due to the lack of familiarity with the rival.

A shortcoming of our study is that our experimental protocol provided information on memory for unfamiliar/familiar individuals but not on memory for unique, equally well-known individuals with whom the subject may have had different experiences. Therefore, our cautious, although provisional, conclusion is that we have not demonstrated a 'true' individual recognition, but simply *P. longicarpus*' capability of a binary discrimination between conspecifics.

Indeed, expt 3 clearly reveals that hermit crabs still classify a conspecific as familiar after having interacted with five other individuals for one full-day. In other words, experiences with different crabs are not sufficient to erase the memory of a former rival, at least after 1 d of separation. This is an intriguing result, since, on the one hand, it suggests that the binary system of individual discrimination is more refined than previously shown and, on the other, it hints at the hermit crab potential for recognizing the opponents as identities, and not simply as categories.

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Literature Cited

Alexander, R. D. 1961: Aggressiveness, territoriality, and sexual behaviour in field crickets. Behaviour **17,** 130—223.

Allee, W. C. & Douglis, M. B. 1945: A dominance order in the hermit crab, *Pagurus longicarpus* Say. Ecology **26,** 411—412.

Angel, J. E. 2000: Effects of shell fit on the biology of the hermit crab *Pagurus longicarpus* (Say). J. Exp. Mar. Biol. Ecol. **243,** 169—184.

Barnard, C. J. & Burk, T. 1979: Dominance hierarchies and the evolution of 'individual recognition'. J. Theor. Biol. **81,** 65—73.

Barrows, E. M., Bell, W. J. & Michener, C. D. 1975: Individual odor differences and their social functions in insects. Proc. Natl. Acad. Sci. U.S.A. **72,** 2824—2828.

Beecher, M. D. 1989: Signalling systems for individual recognition: an information theory approach. Anim. Behav. **38,** 248—261.

Bell, W. J. 1974: Recognition of resident and non-resident individuals in intraspecific nest defense of a primitively eusocial halictine bee. J. Comp. Physiol. **93,** 195—202.

Boal, J. G. 1996: Absence of social recognition in laboratory-reared cuttlefish, *Sepia officinalis* L. (Mollusca: Cephalopoda). Anim. Behav. **52,** 529—537.

Caldwell, R. L. 1979: Cavity occupation and defensive behaviour in the stomatopod *Gonodactylus festae*: evidence for chemically mediated individual recognition. Anim. Behav. **27,** 294—301.

Caldwell, R. L. 1985: A test of individual recognition in the stomatopod *Gonodactylus festae*. Anim. Behav. **33,** 101—106.

Caldwell, R. L. 1992: Recognition, signalling and reduced aggression between former mates in a stomatopod. Anim. Behav. **44,** 11—19.

Carew, T. J. & Sahley, C. L. 1986: Invertebrate learning and memory: from behaviour to molecules. Ann. Rev. Neurosci. **9,** 435—487.

Dugatkin, L. A. 1997: Winner and loser effects and the structures of dominance hierarchies. Behav. Ecol. **8,** 583—587.

Dunham, P. J. 1972: Some effects of group housing upon the aggressive behavior of the lobster *Homarus americanus*. J. Fish. Res. Board Can. **29,** 598—601.

Gherardi, F. & Daniels, W. H. 2003: Dominance hierarchies and status recognition in the crayfish, *Procambarus acutus acutus*. Can. J. Zool. **81,** 1269—1281.
Gherardi, F. & Tiedemann, J. 2004a: Binary individual recognition in hermit crabs. Behav. Ecol. Sociobiol. **55,** 524—530.
Gherardi, F. & Tiedemann, J. 2004b: Chemical cues and binary individual recognition in the hermit crab, *Pagurus longicarpus*. J. Zool. Lond. **263,** 23—29.
Grant, W. C. Jr. & Ulmer, K. M. 1974: Shell selection and aggressive behavior in two sympatric species of hermit crabs. Biol. Bull. **146,** 32—43.
Hazlett, B. A. 1966: Factors affecting the aggressive behavior of the hermit crab *Calcinus tibicen*. Z. Tierpsychol. **23,** 655—671.
Hazlett, B. A. 1969: 'Individual' recognition and agonistic behaviour in *Pagurus bernhardus*. Nature **222,** 268—269.
Jackson, N. W. & Elwood, R. W. 1989: Memory of information gained during shell investigation by the hermit crab, *Pagurus bernhardus*. Anim. Behav. **37,** 529—534.
Johnson, V. R. Jr. 1977: Individual recognition in the banded shrimp *Stenopus hispidus*. Anim. Behav. **25,** 418—428.
Kaiser, L., Pérez-Maluf, R., Sandoz, J. C. & Pham-Delègue, M. H. 2003: Dynamics of odour learning in *Leptopilina boulardi*, a hymenopterous parasitoid. Anim. Behav. **66,** 1077—1084.
Karavanich, C. & Atema, J. 1998: Individual recognition and memory in lobster dominance. Anim. Behav. **56,** 1553—1560.
Linsenmair, K. E. 1972: Die Bedeutung familienspezifischer 'Abzeichen' für den Familienzusammenhalt bei der sozialen Wüstenassel *Hemilepistus reaumuri* Audouin u. Savigny (Crustacea, Isopoda, Oniscoidea). Z. Tierpsychol. **31,** 131—162.
Linsenmair, K. E. 1984: Comparative studies on the social behaviour of the desert isopod *Hemilepistus reaumuri* and a Canarian *Porcellio* species. Symp. Zool. Soc. Lond. **53,** 423—453.
Linsenmair, K. E. 1985: Individual and family recognition in subsocial arthropods, in particular in the desert isopod *Hemilepistus reaumuri*. Fortschr. Zool. **31,** 411—436.
Lowe, M. E. 1956: Dominance-subordinance relationships in the crawfish *Cambarellus shufeldtii*. Tulane Stud. Zool. **4,** 139—170.
Menzel, R., Manz, G., Menzel, R. & Greggers, U. 2001: Massed and spaced learning in honeybees: the role of CS, US, the inter-trial interval and the test trial. Learn. Mem. **8,** 198—208.
Pechenik, J. A. & Lewis, S. 2000: Avoidance of drilled gastropod shells by the hermit crab *Pagurus longicarpus* at Nahant, Massachusetts. J. Exp. Mar. Biol. Ecol. **253,** 17—32.
Rahman, N., Dunham, D. W. & Govind, C. K. 2001: Mate recognition and pairing in the big-clawed snapping shrimp, *Alpheus heterochelis*. Mar. Fresh. Behav. Physiol. **34,** 213—226.
Rebach, S. 1978: The role of celestial cues in short range migrations of the hermit crab, *Pagurus longicarpus*. Anim. Behav. **26,** 835—842.
Rittschof, D. 1980: Chemical attraction of hermit crabs and other attendants to gastropod predation sites. J. Chem. Ecol. **6,** 103—118.
Rufino, M. M. & Jones, D. A. 2001: Binary individual recognition in *Lysmata debelius* (Decapoda: Hippolytidae) under laboratory conditions. J. Crust. Biol. **21,** 388—392.
Schreirer, C. J., Ray, W. S. & Hare, N. 1976: The analysis of ranked data derived from completely randomized factorial designs. Biometrics **32,** 429—434.
Scully, E. P. 1978: Utilization of surface foam as a food source by the hermit crab, *Pagurus longicarpus* Say, 1817. Mar. Behav. Physiol. **5,** 159—162.
Scully, E. P. 1979: The effects of gastropod shell availability and habitat characteristics on shell utilization by the intertidal hermit crab *Pagurus longicarpus* Say. J. Exp. Mar. Biol. Ecol. **37,** 139—152.
Seelinger, G. & Seelinger, U. 1983: On the social organisation, alarm and fighting in the primitive cockroach *Cryptocercus punctulatus* Scudder. Z. Tierpsychol. **61,** 315—333.
Seibt, U. & Wickler, W. 1979: The biological significance of the pair-bond in the shrimp *Hymenocera picta*. Z. Tierpsychol. **5,** 166—179.
Siegel, S. & Castellan, N. J. Jr. 1988: Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill, New York.
Tibbetts, E. A. 2002: Visual signals of individual identity in the wasp *Polistes fuscatus*. Proc. R. Soc. Lond. B **269,** 1423—1428.

Vannini, M. & Gherardi, F. 1981: Dominance and individual recognition in *Potamon fluviatile* (Decapoda, Brachyura): Possible role of visual cues. Mar. Behav. Phys. **8,** 13—20.
Wilber, T. P. Jr. 1989: Associations between gastropod shell characteristics and egg production in the hermit crab *Pagurus longicarpus*. Oecologia **81,** 6—15.
Wilber, T. P. Jr. & Herrnkind, W. 1982: Rate of new shell acquisition by hermit crabs in a salt marsh habitat. J. Crust. Biol. **2,** 588—592.
Wilber, T. P. Jr. & Herrnkind, W. 1984: Predaceous gastropods regulate new-shell supply to salt marsh hermit crabs. Mar. Biol. **79,** 145—150.
Williams, A. B. 1984: Shrimps, Lobsters, and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, DC.
Winston, M. & Jacobson, S. 1978: Dominance and effects of strange conspecifics on aggressive interactions in the hermit crab *Pagurus longicarpus*. Anim. Behav. **26,** 184—191.
Zar, J. H. 1984: Biostatistical Analysis. Prentice Hall, Englewood Cliffs, NJ.
Zulandt Schneider, R. A., Huber, R. & Moore, P. A. 2001: Individual and status recognition in the crayfish, *Orconectes rusticus*: the effects of urine release on fight dynamics. Behaviour **138,** 137—153.

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