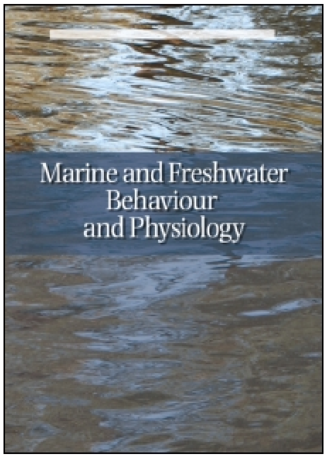
Can hermit crabs recognize social partners by odor? And why?

Original Citation:

Can hermit crabs recognize social partners by odor? And why? / F. GHERARDI; E. TRICARICO. - In: MARINE AND FRESHWATER BEHAVIOUR AND PHYSIOLOGY. - ISSN 1023-6244. - STAMPA. - 40:(2007), pp. 201-212. [10.1080/10236240701562297]

Published version:
DOI: 10.1080/10236240701562297



Marine and Freshwater Behaviour and Physiology

Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713644420

Can hermit crabs recognize social partners by odors? And why?

Francesca Gherardi [a]; Elena Tricarico [a]
[a] Dipartimento di Biologia Animale e Genetica, University of Florence, Florence, Italy

Online Publication Date: 01 September 2007
To cite this Article: Gherardi, Francesca and Tricarico, Elena (2007) 'Can hermit crabs recognize social partners by odors? And why?', Marine and Freshwater Behaviour and Physiology, 40:3, 201 - 212
To link to this article: DOI: 10.1080/10236240701562297
URL: http://dx.doi.org/10.1080/10236240701562297

Marine and Freshwater Behaviour and Physiology
September 2007; 40(3): 201–212

Can hermit crabs recognize social partners by odors? And why?

FRANCESCA GHERARDI & ELENA TRICARICO

Dipartimento di Biologia Animale e Genetica, University of Florence, Florence. Italy

(Received 31 December 2006; in final form 8 July 2007)

Abstract
Individual recognition, i.e., the ability of an animal to recognize the identity of a conspecific, is a key element in the social life of many vertebrates. This phenomenon has rarely been investigated in invertebrates, particularly in pre-social arthropods, and is generally poorly understood for several reasons, including (1) the disparity between what the experiments actually demonstrated and what we implicitly mean by individual recognition, (2) the limited knowledge of the sensory channels used to recognize the social partner (particularly in the case of pre-social arthropods), and (3) the general disregard for the nature of representations that an animal constructs concerning the recognized conspecific. This article aims to review what is currently known about individual recognition mediated by pheromones in the shallow-water hermit crab *Pagurus longicarpus*. Methodological biases, on one hand, and promises of future success, on the other, are pinpointed while explaining the results obtained so far. Finally, an adaptive explanation is offered that attempts to solve the observed hiatus between the "virtuosism" shown by *P. longicarpus* in the laboratory and the apparent simplistic way of shell recruitment used in the field. Individual recognition, even if its expression is very rare in nature, might be a matter of life or death for the hermit crab that makes recourse to it.

Keywords: *Individual recognition, chemical cues, aquatic environments, hermit crabs,* Pagurus longicarpus

Introduction

Individual recognition, meaning the ability of an animal to recognize the identity of a conspecific, is a key element in the social life of a multitude of species. Because of its property of assessing unique cues, it is likely to be a complex task requiring specific perception and discrimination abilities (Mateo 2004). Nevertheless, individual recognition brings considerable benefits, particularly if animals can remember and use information from previous encounters to moderate future responses toward the same individuals (Thom and Hurst 2004). It plays a relevant role in mate selection, pair bonds, territorial defense, dominance, and other social and pre-social contexts (Zayan 1994) in several vertebrates (e.g., Halpin 1980; Hojesjo et al. 1998; Bonadonna and Nevitt 2004), whereas there are

---

Correspondence: Francesca Gherardi, Dipartimento di Biologia Animale e Genetica, University of Florence, Via Romana 17, 50125, Firenze. Italy. E-mail: francesca.gherardi@unifi.it

ISSN 1023–6244 print/ISSN 1029–0362 online/07/030201–212 © 2007 Taylor & Francis
DOI: 10.1080/10236240701562297

only a few invertebrates, particularly arthropods, where this phenomenon has been investigated (Table I). More abundant on the contrary are the reports of self/nonself recognition systems. These have been described in a wide range of marine taxa (sponges, cnidaria, and tunicates; Hildemann et al. 1979) and in arthropods (references in Tsutsui 2004). Indeed, the development of mechanisms that permit kin to be distinguished from unrelated individuals is subject, particularly in eusocial insects, to strong selection pressure to direct altruistic behaviors towards relatives (cf. Hölldobler and Wilson 1990).

When individual recognition occurs, sexual partners, nest-mates, and family groups are most often found to rely on it when they interact with each other (Table I), whereas there are few reports suggesting that arthropods use it in aggressive contests.

The general lack of knowledge about this phenomenon is made even worse by the disparity between what the experiments actually demonstrated and what we implicitly mean by individual recognition (Johnston and Jernigan 1994). Indeed, the question of whether the discrimination being made is between unique, known individuals or between categories of individuals has rarely been raised (Thom and Hurst 2004). In the majority of cases, the methods employed measure differences in the response of an animal to two familiar individuals (or signals from them) compared with novel or relatively unfamiliar individuals, where for "familiar" (and "unfamiliar") we mean here an individual that had been previously met (and not). Results of such experiments thus should document a discrimination between "heterogeneous subgroups" (Barrows et al. 1975) in the form of a "binary" individual recognition (Archawaranon et al. 1991), but do not demonstrate the ability of an animal to recognize one out of many, known individuals from "a unique set of cues", as required by a "true" individual recognition (Beecher 1989).

The poor understanding of this phenomenon, especially in the case of pre-social arthropods, is exacerbated by both the scarce knowledge we have of the sensory channel or channels (in the case of a multimodal system of communication; Partan and Marler 2005) used to recognize the social partner and the general disregard for the nature of representations or memory that an animal constructs of the recognized conspecific.

This article aims to review what we know (and what we do not) about the phenomenon of individual recognition in pre-social aquatic arthropods, using the hermit crab *Pagurus longicarpus* Say as a model organism. The constraints posed by the adopted methodology in the ongoing research, on one hand, and the promises of future success, on the other, will be pinpointed while explaining the results obtained so far.

The long-clawed hermit crab, *P. longicarpus*

Hermit crabs are optimal model organisms to investigate mechanisms of individual recognition. The ability to recognize individuals was first suggested by Hazlett (1969) for *P. bernhardus* and, in the form of a binary individual recognition, was subsequently described in *P. longicarpus* (Gherardi and Tiedemann 2004a), a common species inhabiting shallow waters of the Atlantic coasts of North America (Williams 1984). In this experiment, the authors excluded the possibility that this species was able to recognize familiar from unfamiliar shells, rather than conspecifics (see, on the contrary, Jackson and Elwood 1989). Later, Gherardi and Atema (2005b) showed that hermit crabs recognize a social partner after a brief exposure to the stimulus animal (30 min) and that memory of the conspecific lasts for a relatively long time (between 4 and 6 d).

Binary individual recognition was assumed to be in hermit crabs a means to maintain stable hierarchical relationships, which therefore should be more properly classified as

Table I. List of arthropods where individual recognition has been investigated.

	Species	Context	Individuals recognized	Sensory channel	Badge	Reference
Crustacea, Decapoda	*Alpheus heterochelis*	Mate recognition	Sexual partners	Chemical	Undetermined	Rahman et al. 2001
	Cambarellus shufeldtii	Dominance hierarchy	Opponents	Undetermined	Undetermined	Lowe 1956
	Gonodactylus bredini	Mate recognition	Sexual partners	Chemical	Undetermined	Caldwell 1992
	Gonodactylus festai	Dominance hierarchy	Opponents	Chemical	Undetermined	Caldwell 1979, 1985
	Homarus americanus	Dominance hierarchy	Opponents	Chemical	Undetermined	Karavanich and Atema 1998
	Hymenocera picta	Mate recognition	Sexual partners	Chemical	Undetermined	Seibt and Wickler 1979
	Lysmata debelius	Mate recognition	Sexual partners	Undetermined	Undetermined	Rufino and Jones 2001
	Pagurus bernhardus	Dominance hierarchy	Opponents	Undetermined	Undetermined	Hazlett 1969
	Pagurus longicarpus	Dominance hierarchy	Opponents	Chemical	Undetermined	Gherardi and Tiedemann 2004a
	Potamon fluviatile	Dominance hierarchy	Opponents	Visual	General appearance	Vannini and Gherardi 1981
	Stenopus hispidus	Mate recognition	Sexual partners	Chemical	Undetermined	Johnson 1977
	Synalpheus regalis	Colony	Nest-mates	Chemical	Undetermined	Duffy et al. 2002
	Uca capricornis	Mate recognition	Sexual partners	Visual	Carapace color	Detto et al. 2006
Crustacea, Isopoda	*Cryptocercus punctulatus*	Family groups	Family members	Chemical	Undetermined	Seelinger and Seelinger 1983
	Hemilepistus reaumuri	Family groups	Family members	Chemical	Undetermined	Linsenmair 1972, 1985
	Hemilepistus reaumuri	Mate recognition	Sexual partners	Chemical	Undetermined	Linsenmair 1985
	Porcellio sp.	Family groups	Family members	Chemical	Undetermined	Linsenmair 1984
Insecta, Hymenoptera	*Lasioglossum zephrym*	Colony	Nest-mates	Chemical	Undetermined	Bell 1974
	Pachycondyla villosa	Colony	Founding queens	Chemical	Undetermined	D'Ettorre and Heinze 2005
	Polistes dominulus	Colony	Founding queens	Visual	Body markings	Baracchi et al. 2006
	Polistes fuscatus	Colony	Nest-mates	Visual	Body markings	Tibbetts 2002

"assessment" hierarchies (Barnard and Burk 1979). Indeed, *P. longicarpus* is known to form dominance hierarchies in captivity (Allee and Douglis 1945; Winston and Jacobson 1978), but repeated contacts among a small number of individuals were shown to occur also in the field, where crabs aggregate around gastropod predation sites (Scully 1978; Rittschof 1980; Tricarico and Gherardi 2006). These small aggregations seem to persist in the same place for a relatively long time, between a few hours and 2 days (Tricarico and Gherardi 2006). All this information, taken together, suggests that social life is complex enough in this species to warrant a form of recognition.

Individual recognition is mediated by pheromones

A number of behavioral studies showed that olfaction can be used by hermit crabs in many contexts. Several species display adaptive behaviors when exposed to odors that signal shell availability (e.g., Rittschof 1980; Rittschof et al. 1992) and, as found in *P. bernhardus*, seem to recognize some pheromones released in the water by fighting conspecifics (Briffa and Williams 2006).

When offered empty gastropod shells, crabs perform a series of investigatory acts (e.g., Elwood and Stewart 1985; Jackson and 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. Pheromones in the medium usually affect the investigatory responses of crabs towards shells either occupied by conspecifics (Hazlett 1996a, 1996b; Rittschof and Hazlett 1997; Hazlett 2000) or empty (Gherardi and Atema 2005a), so that shell investigation has the potential of being used as a reliable bioassay to reveal chemical detection by hermit crabs. Although this approach cannot show temporal structure or elements of directionality in the release of chemical cues, it is a noninvasive means of determining, in a simple way, whether they are used (Briffa and Williams 2006). This bioassay was first used by Hazlett (1990) to demonstrate the presence of a disturbance pheromone in the hermit crab *Calcinus laevimanus* and more recently by Gherardi and Tiedemann (2004b) to reveal the ability of *P. longicarpus* to recognize conspecifics by smell.

Specifically, Gherardi and Tiedemann (2004b) analyzed the response to a target shell exhibited by test crabs in three different contexts, where test animals could (1) see only, (2) smell only, or (3) see and smell one conspecific. Conspecifics were either known (familiar conspecifics, FC) or unknown (unfamiliar conspecifics, UC) individuals that were of the same status (dominant or subordinate) as the former opponents. As a control, the behavior of the test crabs was analyzed in the absence of any stimulus emitted by a conspecific (but in the presence of the test crab's odor alone).

The adoption of this protocol allowed the authors to explore the communicative consequences of combining signal components from visual and olfactory channels, given that previous studies (Hazlett 1982; Diaz et al. 1994; Chiussi et al. 2001) had shown that hermit crabs may make use in complex ways of chemical and visual stimuli, at least when these stimuli are associated with particular types of shells.

The results of this study confirmed the ability of this species to discriminate between familiar and unfamiliar individuals (Gherardi and Tiedemann 2004a), but also showed that only when the crabs were allowed to smell a conspecific did they exhibit responses which were stronger in the presence of unfamiliar than familiar stimuli (Figure 1): latency was longer and the approaches to the shell were more frequent in FC than in UC conditions in both the "smell only" and the "sight and smell" treatments, but not in the "sight only" treatment. However, chemical and visual stimuli from an unfamiliar individual, if presented

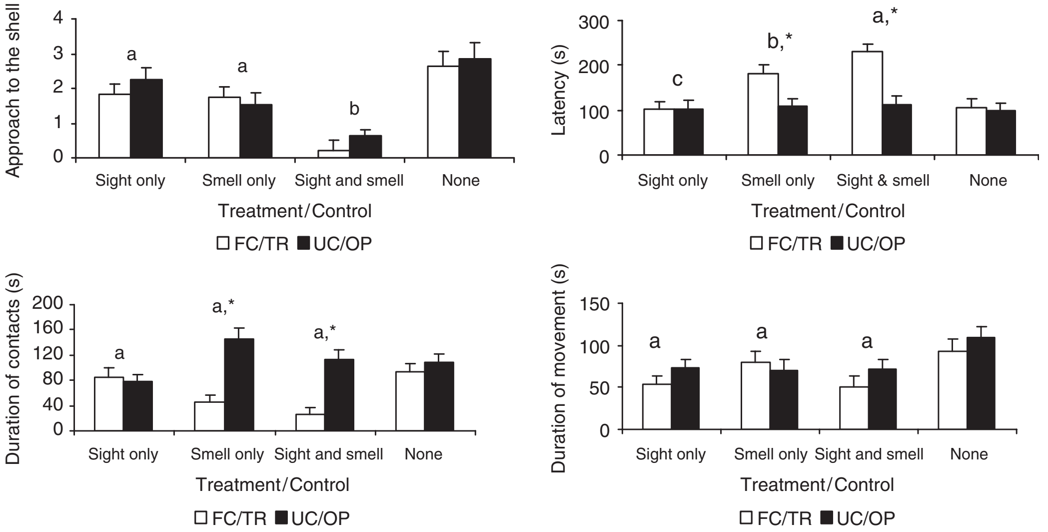


Figure 1. Sensorial channel/s used by hermit crabs to recognize familiar conspecifics (after Gherardi and Tiedemann 2004b). A test crab was offered with a target shell under three treatments, "sight only", "smell only", and "sight and smell", in which it was presented to visual, chemical, and visual plus chemical stimuli, respectively, emitted by a conspecific. Conspecifics were either known individuals (familiar conspecifics, FC) or unknown individuals (unfamiliar conspecifics, UC) that were however of the same status (dominant or subordinate) as the former opponents. As a control, the test crab was placed in the absence of any stimuli. The experimental apparatus consisted of plastic bowls containing 160 cc artificial seawater (salinity: 27 ppt and temperature: 22°C) divided by a transparent (TR) or opaque (OP) sector into two compartments, one for the nontest crab and the other for the test crab (with the target shell). Treatments differed for (1) the sector which was either TR (in the "sight only" and "sight and smell" treatments) or OP (in the "smell only" treatment) and (2) the seawater in the test crab's compartment, which was conditioned either by the test crab's odor only (in the "sight only" treatment) or by the nontest crab's odor (in the "smell only" and "sight and smell" treatments). In the control, seawater was conditioned by the test crab's odor only and the sector was either TR or OP. The figure shows mean (+SE) values of four behavioral parameters recorded during 5 min of observation, compared between FC and UC. The recorded parameters were: the number of approaches to the target shell, the time passed between the test crab's insertion into the compartment and its first approach to the target shell (latency), the time spent interacting with the target shell, and the time spent in locomotion. For each parameter, N are 40 for FC/TR and 40 for UC/OP. Letters indicate the hierarchy among treatments (after a Kruskal–Wallis one-way analysis of variance followed by a Multiple comparison test); the asterisk means a significant difference between conditions (at least, $P < 0.05$, after a Mann–Whitney ranks test).

together, sometimes elicited different responses than only its smell. In fact, only in the "sight and smell" treatment was the number of approaches to the shell significantly higher in UC than in FC conditions. Besides, crabs appeared less reactive (longer latencies and lower number of approaches to the shell) in the presence of both the smell and the sight of a conspecific than at its smell only. In summary, olfaction appears to be the dominant sensory channel in the binary discrimination of *P. longicarpus*, but the potential of its integration with visual stimuli cannot be excluded, supporting the idea that communication is multimodal (Partan and Marler 2005) also in the context of individual recognition.

Gherardi and Tiedeman's (2004a) study also showed that individuals of *P. longicarpus* are able to discriminate the odor of a conspecific within the complex olfactory environment in which they live, including the chemicals emitted by the shells. Also, their own odor seemed to be distinguished from the odor of either a familiar or an unfamiliar conspecific, as was apparent from the less intense responses exhibited by crabs in the control than in the treatments (Figure 1). Taken together, these results might suggest that in this species chemical recognition is more refined than a binary identification and that chemical ''badges'' can be the attributes of individual crabs. Gherardi and Atema (2005b) came to a similar conclusion when they found that hermit crabs are still able to classify a conspecific as familiar after having experienced 1-day interactions with other individuals. In other words, experiences with different crabs (and possibly with different odors, all familiar) are not sufficient to erase the memory of a former rival, at least after one day of separation.

Indeed, a test for a true individual recognition would involve different responses to two equally-known individuals (Johnston and Jernigan 1994). A test meeting this requirement was first used for aquatic invertebrates by Caldwell (1985), who showed that the cavity-dwelling stomatopod *Gonodactylus festae* responds differently to the odor of two familiar individuals and that this difference is based on previous experience with its opponents. Intruders rapidly entered cavities containing the odor of the residents they had previously defeated, but were hesitant to enter cavities containing the odor of the residents that had on the contrary defeated them. Similarly, by monitoring responses to a target shell exhibited by a test *P. longicarpus* in the presence of odors of four different proveniences (test crab; unfamiliar conspecifics; familiar conspecifics that won previous fights with the test crab, α; and familiar conspecifics that lost previous fights with the test crab, γ), Gherardi et al. (2005) found that hermit crabs can chemically discriminate (1) between themselves and others and (2) between at least two familiar individuals, the winner and the loser. Because test crabs seemed not to discriminate among unfamiliar crabs with the same winning/losing experience and morphological attributes as familiar crabs, the ability to chemically recognize at least two different familiar individuals was not due to odors associated with a rank, a size class, or a shell type, but was related to the experience that test crabs have had with those previously encountered individuals.

The results of this experiment are not, however, unequivocal in proving the existence of a true individual recognition in hermit crabs. A shortcoming is that what has really been shown is that *P. longicarpus* can distinguish between the odors of ''animals defeated'' and ''animals by which it has been defeated'', whereas its ability to discriminate between two animals that had both won and both lost would have been a better demonstration of a true individual recognition in this species. It seems difficult, if not impossible however, to develop an appropriate experimental protocol that could produce such a distinction at least using behavioral bioassays (see Thom and Hurst 2004 for a discussion of the different experimental paradigms used to assess individual recognition ability).

The odor of an individual is associated with the quality of its shell

Individual recognition is a sophisticated cognitive function. True individual recognition, in fact, requires the association of some individually distinct information with memories of past experiences (Johnston and Bullock 2001). There are several characteristics that make the task different from standard learning (Lai and Johnston 2002), as it is also evident in hermit crabs. First, *P. longicarpus* does not need to be trained over many repeated trials; rather, it shows evidence of recognition after only one or a few brief exposures to stimulus animals, less than 30 min (Gherardi and Atema 2005b). Second, hermit crabs do not require specific training but show evidence of recognition without external, experimenter-provided reinforcement or punishment. Third, although memory for individuals can be acquired in a few minutes, it lasts for a relatively long time (about five days) without further exposure to the stimulus animal (Gherardi and Atema 2005b).

The results of previous experiments on *P. longicarpus* had suggested that, during the familiarization, the receiver might associate the odor from a social partner with one of its relevant attributes, either the rank, the size, or the quality of its shell (or with a combination of these three attributes). This hypothesis was tested by Gherardi et al. (2005) in three experiments, in which triplets of crabs that differed for a single attribute, the other being equal, were first subject to a 24-h familiarization phase. Then, the crabs with the intermediate attribute, β crabs (the receivers), were offered in random succession with the target shell in the presence of the odor of familiar α and γ crabs, which had the same size and shell quality as the receiver in a first experiment, a different size (being either larger or smaller) but the same shell quality in a second experiment, and the same size but a shell of either lower or higher quality than the receiver's in a third experiment. The results clearly illustrated that *P. longicarpus* can associate the odor from a conspecific with the quality of the shell it occupies and reacts accordingly in the presence of a target shell (Figure 2). It seems likely that during the familiarization phase individual odors became labels of shell quality; if these labels indicated a high shell quality,

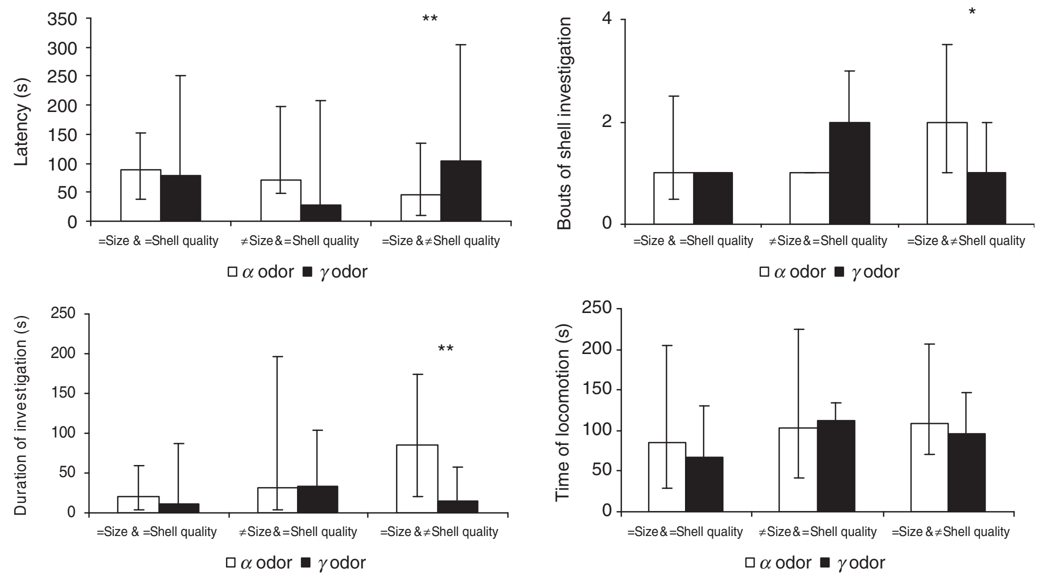


Figure 2. Association between the odor of a familiar conspecific and three of its attributes (rank, body size, and shell quality) (after Gherardi et al. 2005). The experiments consisted in monitoring the response of a test crab to a target shell as in Figure 1 in the presence of seawater conditioned by the odor of two familiar conspecifics (α and γ crabs), analyzed separately for 5 min each in random order. Three conditions were examined: same body size and same shell quality (1), different body size and same shell quality (2), and same body size and different shell quality (3). α (and γ) was the dominant (and subordinate) crab in (1), the bigger (and the smaller) crab in (2), and the crab occupying a larger-than-optimal (and a smaller-than-optimal) shell in (3). The figure shows median values (and interquartile ranges) of latency (see Figure 1), bouts of investigation of the target shell, the time spent investigating the target shell, and the time spent in locomotion. * and ** denote $P < 0.05$ and $P < 0.01$, respectively, after a Friedman two-way analysis of variance.

their detection evoked an intense shell investigation when the receivers were presented with a high quality shell; otherwise, shell investigation would have been scarce or absent. This view has been supported by a companion experiment revealing a plasticity of individual odor-shell quality association (Figure 3). Once an individual crab had switched to a shell of a different quality, responses to the offered shell were consistent with the changed association. In fact, shell investigation was strong in the presence of the odor of a former γ occupying a high quality shell and weak in the presence of a former α occupying a low quality shell.

These results are instructive in suggesting that what the odor of a familiar individual means to a hermit crab is the quality of the shell the social partner inhabits, independently of its size and rank. Hermit crabs seem to associate a type of information emitted by the social partner (e.g., chemical cues) with some experiences with it (e.g., exploration of its shell) and keep this association for a relatively long time. In other words, they seem to have a "concept" of other individuals and behave accordingly, in a very adaptive fashion, as illustrated below.

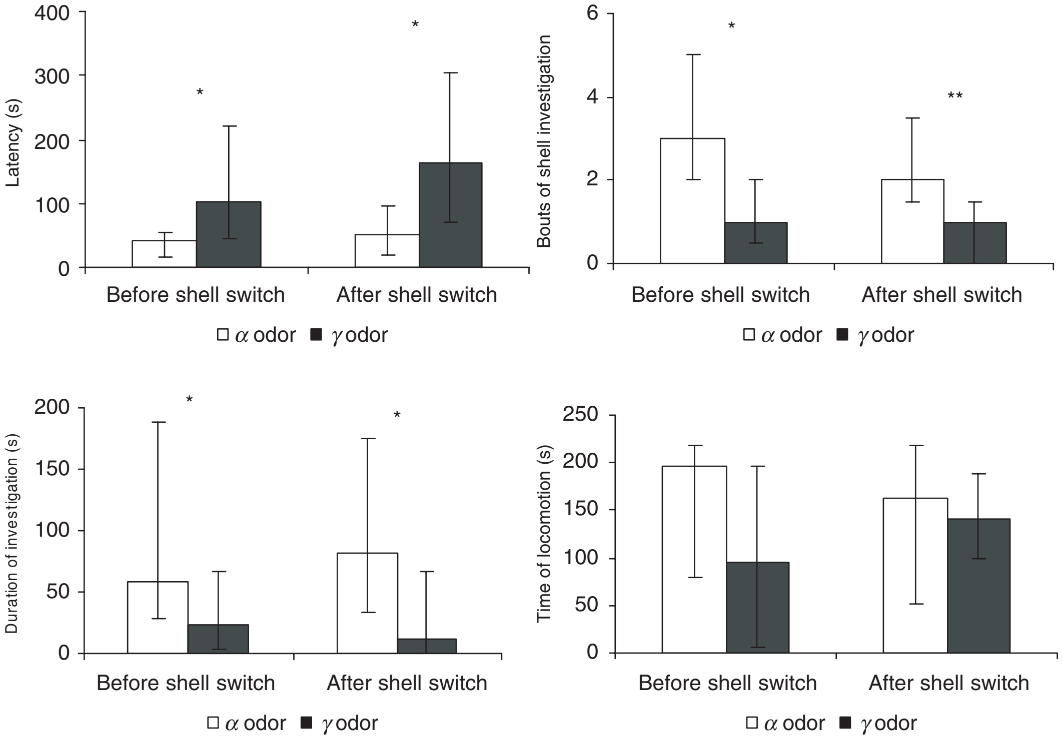


Figure 3. Plasticity of the association between the odor of a familiar conspecific and the quality of its shell (after Gherardi et al. 2005). The experiment consisted in monitoring the test crab's behavior when the familiar conspecific had been forced to occupy a shell of opposed quality with respect to the shell it occupied previously, so that the crabs occupying larger-than-optimal shells (α crabs) and smaller-than-optimal shells (γ crabs) of Figure 2 had become γ and α crabs, respectively. The figure shows median values (and interquartile ranges) of the four parameters as in Figure 2, compared before and after shell switches. In the figure, α (and γ) crabs are the individuals that were previously ranked γ (and α) crabs. * and ** denote $P < 0.05$ and $P < 0.01$, respectively, after a Wilcoxon matched-pairs signed-ranks test.

It has been abundantly proven that the survival, growth, protection, and reproduction of this taxon strictly depend on the occupancy of gastropod shells of appropriate size and shape (e.g., Fotheringham 1976; Bertness 1981; Elwood et al. 1995). Empty shells (hermit crabs are unable to directly prey on living snails; see, Rutheford 1977, for an exception) are in acutely short supply in the habitat (e.g., Scully 1979). Most often, they can be found following snail death at gastropod predation sites (e.g., Rittschof 1980; Tricarico and Gherardi 2006), where hermit crabs may aggregate and form dominance hierarchies. The dominant crab obtains the first opportunity to occupy an empty shell as it is released by a predator; afterwards, the other individuals may exchange shells down the hierarchy. Therefore, these aggregations function as ''shell markets'' and benefit a large number of site attendants (Rittschof et al. 1992) as the result of a vacancy chain process (Chase et al. 1988). Having obtained a high quality shell, a crab generally leaves the predation site (Rittschof 1980), thus subtracting the shell from the market. It would therefore be advantageous for an individual to classify the quality of the shells inhabited by the other attendants rapidly and then to spend time combating or negotiating (Hazlett 1978) for a really good shell.

Due to water turbidity typical of many salt marsh habitats, chemical cues signaling shell quality might provide more reliable information than visual stimuli emitted by the shell itself; on the other hand, the exclusive use of tactile information from the shell would require time and energy consumption in repeated investigatory acts. Indeed, *P. longicarpus* quickly learns the chemical identity of a social partner (Gherardi and Atema 2005b), is inaccurate in discriminating shells by sight (Gherardi and Tiedeman 2004a), and often switches shells without prior investigation (Scully 1986). In this scenario, the plastic nature of the association between the individual odor of a conspecific and the quality of its shell has a clear adaptive value. Obviously, any shell exchange breaks the link between a given hermit crab and a given shell, and the aggregations of hermit crabs around gastropod predation sites are characterized by a cascade of shell switches. Therefore, the plastic response to the cues associated with high quality shells is a key factor in optimizing shell acquisition and reducing errors.

Individual recognition can increase survival and fitness

For at least three reasons, our interpretation above concerning the benefits of individual recognition to hermit crabs should be, at least in part, revised. First, as lamented by Atema and Steinbach (2007) for all crustaceans, a glaring gap in knowledge is the general lack of information about the chemical identity of pheromones. The refined behavior shown by hermit crabs suggests complexities rivaling those in social insects, but, unless the chemistry catches up with the biology, ''we will remain ignorant about the true extent of chemical signaling'' (Atema and Steinbach 2007).

Second, how the information on individual identity is coded depends on whether an animal benefits from advertising it (Thom and Hurst 2004). If there is no advantage to being recognized, the animal is unlikely to deliberately reveal its identity and the cue used by the conspecifics to identify it may primarily serve other signaling functions or may have no role in any type of signaling. In hermit crabs, the ''signaler'' seems not to benefit from being recognized (its recognition may increase the risks of being stolen of a high-quality shell), so individual recognition in this taxon does not meet the requirements of a real ''communication''. It can be classified, on the contrary, as a form of ''eavesdropping''

(Bradbury and Vehrencamp 1998), where the recognizing individual is detecting and using information that is not actively signaled to it by the recognized conspecific.

Third, merely demonstrating the ability to distinguish among individuals in the laboratory does not prove that individual recognition is used in the field to mediate interactions among protagonists (Caldwell 1985). To judge the role that individual recognition plays in the ''real world'' of a species, it is essential to understand the ecological and social variables that govern its occurrence. Such data have been in large part obtained for hermit crabs (see above). But a hiatus exists between the ''virtuosism'' shown by *P. longicarpus* in the laboratory and the apparent simplistic way used by this species to recruit shells in the field. After many hours of field work in a salt marsh in New England, Tricarico and Gherardi (2006) never observed shell exchanges between crabs but recorded relatively few and weak interactions between individuals. This might lead us to conclude that individual recognition is an unexpressed ability of hermit crabs under natural conditions. Alternatively, we may think that, even if a crab uses this ability once in its life and succeeds in occupying a high-quality shell as a result, both its life expectancy and its individual fitness would increase sharply. In other words, individual recognition, even if its expression can be very rare in nature, might be, for the hermit crab that uses it, a matter of life or death.

References

Allee WC, Douglis MB. 1945. A dominance order in the hermit crab, *Pagurus longicarpus* Say. Ecology 26:411–412.

Archawaranon M, Dove L, Wiley RH. 1991. Social inertia and hormonal control of aggression and dominance in white-throated sparrows. Behaviour 118:42–64.

Atema J, Steinbach MA. 2007. Chemical communication in the lobster, *Homarus americanus*, and other decapod Crustacea. In: Duffy JE, Thiel M, editors. Evolutionary ecology of social and sexual systems: Crustaceans as model organisms. Oxford, UK: Oxford University Press, in press.

Baracchi D, Turillazzi S, Cervo R. 2006. Riconoscimento individuale in colonie di *Polistes dominulus*: Il canale visivo. Abstract volume, Conference of the Italian Society of Ethology, Erice, Italy, September 2006, p. 106.

Barnard CJ, Burk T. 1979. Dominance hierarchies and the evolution of ''individual recognition''. J. Theor. Biol. 81:65–73.

Barrows EM, Bell WJ, Michener CD. 1975. Individual odor differences and their social functions in insects. Proc. Nat. Acad. Sci. USA 72:2824–2828.

Beecher MD. 1989. Signalling systems for individual recognition: An information theory approach. Anim. Behav. 38:248–261.

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

Bertness MD. 1981. The influence of shell-type on hermit crab growth rate and clutch size (Decapoda, Anomura). Crustaceana 40:197–205.

Bonadonna F, Nevitt GA. 2004. Partner-specific odor recognition in an Antarctic seabird. Science 306835.

Bradbury JW, Vehrencamp SL. 1998. Principles of animal communication. Sunderland, Mass., USA: Sinauer Associates.

Briffa M, Williams R. 2006. Use of chemical cues during shell fights in the hermit crab *Pagurus bernhardus*. Behaviour 143:1281–1290.

Caldwell RL. 1979. Cavity occupation and defensive behaviour in the stomatopod *Gonodactylus festae*: Evidence for chemically mediated individual recognition. Anim. Behav. 27:294–301.

Caldwell RL. 1985. A test of individual recognition in the stomatopod *Gonodactylus festae*. Anim. Behav. 33:101–106.

Caldwell RL. 1992. Recognition, signalling and reduced aggression between former mates in a stomatopod. Anim. Behav. 44:11–19.

Chase ID, Weissburg M, Dewitt TH. 1988. The vacancy chain process: A new mechanism of resource distribution in animals with application to hermit crabs. Anim. Behav. 36:1265–1274.

Chiussi R, Diaz H, Rittschof D, Forward Jr. RB. 2001. Orientation of the hermit crab *Clibanarius antillensis*: Effects of visual and chemical cues. J. Crust. Biol. 21:593–605.

Detto T, Backwell PRY, Hemmi JM, Zeil J. 2006. Visually mediated species and neighbour recognition in fiddler crabs *(Uca mjoebergi* and *Uca capricornis*). Proc. R. Soc. London B 273:1661–1666.

D'Ettorre P, Heinze J. 2005. Individual recognition in ant queens. Current Biology 15:2170–2174.

Diaz H, Forward Jr RB, Orihuela B, Rittschof D. 1994. Chemically stimulated visual orientation and shape discrimination by the hermit crab *Clibanarius vittatus* (Bosc). J. Crust. Biol. 14:20–26.

Duffy JE, Morrison CL, Macdonald KS. 2002. Colony defense and behavioral differentiation in the eusocial shrimp *Synalpheus regalis*. Behav. Ecol. Sociobiol. 51:488–495.

Elwood RW, Marks N, Dick JTA. 1995. Consequences of shell-species preferences for female reproductive success in the hermit crab *Pagurus bernhardus*. Mar Biol 123:431–434.

Elwood RW, Stewart A. 1985. The timing of decisions during shell investigation by the hermit crab, *Pagurus bernhardus*. Anim. Behav. 33:620–627.

Fotheringham N. 1976. Effects of shell stress on the growth of hermit crabs. J. Exp. Mar. Biol. Ecol. 23:299–305.

Gherardi F, Atema J. 2005a. Effects of chemical context on shell investigation behavior in hermit crabs. J. Exp. Mar. Biol. Ecol. 320:1–7.

Gherardi F, Atema J. 2005b. Memory of social partners in hermit crab dominance. Ethology 111:271–285.

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.

Gherardi F, Tricarico E, Atema J. 2005. Unraveling the nature of individual recognition by odor in hermit crabs. J. Chem. Ecol. 31:2877–2896.

Halpin ZT. 1980. Individual odors and individual recognition: Review and commentary. Biol. Behav. 5:233–248.

Hazlett BA. 1969. 'Individual' recognition and agonistic behaviour in *Pagurus bernhardus*. Nature 222:268–269.

Hazlett BA. 1978. Shell exchanges in hermit crabs: Aggression, negotiation or both? Anim. Behav. 26:1278–1279.

Hazlett BA. 1982. Chemical induction of visual orientation in the hermit crab *Clibanarius vittatus*. Anim. Behav. 30:1259–1260.

Hazlett BA. 1990. Disturbance pheromone in the hermit-crab *Calcinus laevimanus* (Randall, 1840). Crustaceana 58:314–316.

Hazlett BA. 1996a. Organisation of hermit crab behaviour: Responses to multiple chemical inputs. Behaviour 133:619–642.

Hazlett BA. 1996b. Comparative study of hermit crab responses to shell-related chemical cues. J. Chem. Ecol. 22:2317–2329.

Hazlett BA. 2000. Responses to single and multiple sources of chemical cues by New Zealand crustaceans. Mar. Fresh. Behav. Physiol. 34:1–20.

Hildemann WH, Bigger CH, Johnston IS. 1979. Histoincompatibility reactions and allogeneic polymorphism among invertebrates. Transplantation Proceedings 11:1136–1142.

Hojesjo J, Johnsson J, Petersson E, Jarvi T. 1998. The importance of being familiar: Individual recognition and social behavior in sea trout (*Salmo trutta*). Behav. Ecol. 9:445–451.

Hölldobler B, Wilson EO. 1990. The ants. Cambridge, MA: The Belknap Press of Harvard University Press.

Jackson NW, Elwood RW. 1989. Memory of information gained during shell investigation by the hermit crab, *Pagurus bernhardus*. Anim. Behav. 37:529–534.

Johnson Jr. VR. 1977. Individual recognition in the banded shrimp *Stenopus hispidus*. Anim. Behav. 25:418–428.

Johnston RE, Bullock TA. 2001. Individual recognition by use of odours in golden hamsters: The nature of individual representations. Anim. Behav. 61:545–557.

Johnston RE, Jernigan P. 1994. Golden hamsters recognize individuals, not just individual scents. Anim. Behav. 48:129–136.

Karavanich C, Atema J. 1998. Individual recognition and memory in lobster dominance. Anim. Behav. 56:1553–1560.

Lai W-S, Johnston RE. 2002. Individual recognition after fighting by golden hamsters: A new method. Physiol. Behav. 76:225–239.

Linsenmair KE. 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 KE. 1984. Comparative studies on the social behaviour of the desert isopod *Hemilepistus reaumuri* and a Canarian *Porcellio* species. Symp. Zool. Soc. London 53:423–453.

Linsenmair KE. 1985. Individual and family recognition in subsocial arthropods, in particular in the desert isopod *Hemilepistus reaumuri*. Fortschr. Zool. 31:411–436.

Lowe ME. 1956. Dominance-subordinance relationships in the crawfish *Cambarellus shufeldtii*. Tulane Studies Zool. 4:139–170.

Mateo JM. 2004. Recognition systems and biological organization: The perception component of social recognition. Ann. Zool. Fennici 41:729–745.

Partan S, Marler P. 2005. Issues in the classification of multimodal communication signals. Am. Natur. 166:231–245.

Rahman N, Dunham DW, Govind CK. 2001. Mate recognition and pairing in the big-clawed snapping shrimp, *Alpheus heterochelis*. Mar. Fresh. Behav. Physiol. 34:213–226.

Rittschof D. 1980. Chemical attraction of hermit crabs and other attendants to gastropod predation sites. J. Chem. Ecol. 6:103–118.

Rittschof D, Hazlett BA. 1997. Behavioural responses of hermit crabs to shell cues, predator haemolymph and body odour. J. Mar. Biol. Ass. U.K. 77:737–751.

Rittschof D, Tsai DW, Massey PG, Blanco L, Kueber Jr GL, Haas Jr. RJ. 1992. Chemical mediation of behavior in hermit crabs: Alarm and aggregation cues. J. Chem. Ecol. 18:959–984.

Rufino MM, Jones DA. 2001. Binary individual recognition in *Lysmata debelius* (Decapoda: Hippolytidae) under laboratory conditions. J. Crust. Biol. 21:388–392.

Rutheford JD. 1977. Removal of living snails from their shells by a hermit crab. Veliger 19:438–439.

Scully EP. 1978. Utilization of surface foam as a food source by the hermit crab, *Pagurus longicarpus* Say, 1817. Mar. Behav. Physiol. 5:159–162.

Scully EP. 1979. The effects of gastropod shell availability and habitat characteristics on shell utilization by the intertidal crab *Pagurus longicarpus* Say. J. Exp. Mar. Biol. Ecol. 37:139–152.

Scully EP. 1986. Shell investigation behavior of the intertidal hermit crab *Pagurus longicarpus* Say. J. Crust. Biol. 6:749–756.

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.

Thom MD, Hurst JL. 2004. Individual recognition by scent. Ann. Zool. Fennici 41:765–787.

Tibbetts EA. 2002. Visual signals of individual identity in the wasp *Polistes fuscatus*. Proc. R. Soc. London B 269:1423–1428.

Tricarico E, Gherardi F. 2006. Shell acquisition by hermit crabs: Which tactic is more efficient? Behav. Ecol. Sociobiol. 60:492–500.

Tsutsui ND. 2004. Scents of self: The expression component of self/non-self recognition systems. Ann. Zool. Fennici 41:713–727.

Vannini M, Gherardi F. 1981. Dominance and individual recognition in *Potamon fluviatile* (Decapoda, Brachyura): Possible role of visual cues. Mar. Behav. Physiol. 8:13–20.

Williams AB. 1984. Shrimps, lobsters, and crabs of the Atlantic coast of the Eastern United States, Maine to Florida. Washington, DC, USA: Smithsonian Institution Press.

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.

Zayan R. 1994. Individual and social recognition. Amsterdam, The Netherlands: Elsevier, Science Publishers.