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Resource assessment in hermit crabs: the worth of their own shell

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Animals gather information about the quality of a resource through its assessment and behave accordingly as a result of adaptive motivational changes. In the hermit crab *Pagurus longicarpus*, we investigated whether an individual was affected in its motivation to acquire a new shell by the quality of the domicile shell (own resource value [ORV]), of the offered shell (external resource value [ERV]), or of both and asked whether its motivation was altered by the information gathered during shell investigation. We analyzed the behavior of hermit crabs inhabiting shells of differing qualities and compared their willingness to acquire an offered shell—optimal, smaller than optimal, or larger than optimal—by measuring the latency to approach it, the number of shell investigation, and its total duration. Crabs in smaller shells (SSs) approached more quick and often the offered shell, whereas crabs in larger shells investigated the offered shell more thoroughly. The readiness of crabs to approach the offered shell and the extent of its investigation were independent of the ERV but were exclusively affected by the ORV, whereas the number and duration of shell investigation did not change with time as investigation proceeded, except for crabs in SSs. These results suggest that *P. longicarpus*' motivation to acquire a new shell is exclusively influenced by the value of the shell it inhabits rather than by the quality of the shell it is offered and that this species does not gather—or does not use—information about ERV during investigation. *Key words*: assessment, hermit crabs, information, *Pagurus longicarpus*, resource value, shells. [*Behav Ecol*]

In light of the wide variation in quality and quantity of resources available in the habitat, animals have evolved the ability to acquire these resources with minimal waste of time and energy. Resource assessment consists of a process in which the resource cues correlated with some expected gain in fitness are monitored by an animal (Parker and Stuart 1976). To this, adaptive motivational changes follow, leading to “strategy shifts in the individual’s behavior” (Parker and Stuart 1976, p. 1056). As the resource assessment proceeds, animals gather information about the quality of the resource at stake and, from this knowledge, make tactical decisions of whether to persist or to renounce that resource. In other words, the knowledge they constantly acquire about the quality of a resource has the ultimate effect of altering their motivational state.

Hermit crabs are ideal organisms to investigate whether resource assessment might effectively modify an animal’s motivation and to what extent. The survival, growth, and reproduction of this taxon strictly depend on the occupancy of gastropod shells of appropriate size and shape (e.g., Fotheringham 1976a; Bertness 1981b; Elwood et al. 1995). A shell that is, for instance, too small can inhibit the growth of the inhabiting crabs (e.g., Angel 2000), reduces their protection against predators (e.g., Angel 2000) and their survival (e.g., Borjesson and Szelistowski 1989), and affects reproductive success in both sexes (Hazlett 1989; Elwood et al. 1995). By contrast, a shell that is too large makes locomotion energetically wasteful (as found in terrestrial hermit crabs, Herreid and Full 1986) and affects female reproduction (Fotheringham 1980; Hazlett et al. 2005). Shell fit may also alter hermit crabs’ responses to environmental cues and their

general behavior (Katz and Rittschof 1993). Therefore, there is a strong selective pressure for hermit crabs to obtain a shell of the appropriate size.

Empty shells (hermit crabs are unable to directly prey on living snails; for an exception, see Rutheford 1977) are in acutely short supply in the habitat (Provenzano 1960; Vance 1972; Fotheringham 1976b; Kellogg 1976; Scully 1979; for exceptions, see Wilber and Herrnkind 1984; Gherardi et al. 1994). Most often, they can be found after snail death at gastropod predation sites (e.g., Rittschof 1980a, 1980b; Rittschof et al. 1995; Tricarico and Gherardi 2006). Alternatively, shells may be obtained by conspecifics or heterospecifics through negotiation (Hazlett 1978, 1980) or interference competition (Hazlett 1966b). In any case, except for very few instances (Wilber and Herrnkind 1984), appropriate shells are extremely difficult to recruit (Tricarico and Gherardi 2006). As a result, the vast majority of the hermit crab populations studied so far chronically suffers from a reduced growth (e.g., Bach et al. 1976).

An apparently obvious consequence of the vital importance of empty shells for hermit crabs on the one hand, and of their scarce availability on the other, is that these organisms have evolved the ability to make fine distinctions between the quality of a shell found in the habitat, either empty or occupied by conspecifics or heterospecifics, and the current domicile shell (e.g., Hazlett 1981; Jackson and Elwood 1989a). This ability has been confirmed by a large number of studies, mostly conducted in *Pagurus bernhardus*. For instance, escalated shell fights occur in this species when the shell at stake is of a higher quality than the attacker’s domicile shell (Dowds and Elwood 1983). Similarly, individuals enter an empty shell more quickly when there can be an increase in quality (Elwood and Stewart 1985), whereas the speed of rejecting the shell correlates with its unsuitability (Neil and Elwood 1986). Knowledge about the quality of an external shell is obtained by hermit crabs first by the means of sight (Reese 1969; Elwood and Stewart 1985; Jackson and Elwood 1990; Elwood 1995) and later by tactile stimuli acquired during their manipulation of both the

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exterior and the interior of the shell–shell investigation. Shell investigation seems to provide more accurate information than sight alone. In fact, as shown by Jackson and Elwood (1990) and Elwood (1995), when hermit crabs were offered a high-quality shell, the startle responses exhibited when subjected to a disturbing stimulus had a significantly shorter duration after having taken tactile contact with that shell. The increased volume of information hermit crabs gather during shell investigation has the effect of modifying their subsequent behavior as an expression of their altered motivation (Jackson and Elwood 1989a; Elwood 1995; Briffa and Elwood 2001). So, Jackson and Elwood (1990) found that hermit crabs exhibited shorter startle responses to a disturbing stimulus while investigating a shell of good, rather than of poor, quality. Finally, hermit crabs were found to recognize already investigated shells from novel shells, as shown by the shorter duration of investigation when offered with the former (Jackson and Elwood 1989b).

Despite the plethora of studies focused on resource assessment in hermit crabs, the previous literature constantly refers to the idea that changes in motivation and decision making mostly result from the perceived value of the offered resource. On the contrary, the role played by the own resource value (ORV) in altering an animal's motivation to obtain a new shell has been investigated in a relatively small number of species (e.g., *P. bernhardus*, Jackson and Elwood 1990; *Clibanarius vittatus*, Diaz et al. 1994, 1995), notwithstanding recent evidence suggesting that, while fighting, hermit crabs might follow decision rules of the type "ORV dependency" (Gherardi 2006).

The aims of this study were to investigate in *Pagurus longicarpus* 1) the effects on the motivation to acquire a new shell exerted by the quality of both the shell that an individual possesses (ORV) and the shell it has been offered (external resource value [ERV]) and 2) motivational changes possibly induced by the information gathered during shell investigation. To this end, we analyzed the behavior of similarly sized hermit crabs occupying shells of different quality and compared their motivation to acquire an offered shell—optimal, smaller than optimal, or larger than optimal—by measuring both the latency to approach it, the number of shell investigation, and their total duration. We hypothesized that crabs in low-quality shells (i.e., shell smaller or larger than optimal) persist in investigating the experimental shell for longer, particularly when the offered shell is optimal, whereas those in optimal shells (OSs) are less ready to investigate the offered shell and renounce quicker.

MATERIALS AND METHODS

Subjects, collection, and housing conditions

The long-clawed hermit crab, *P. longicarpus* Say 1817, is a common species in shallow waters along the Atlantic coast of the United States of America and in the Gulf of Mexico (Williams 1984). Around 400 individuals with a major chela width (CW) of 0.1–0.5 mm were collected from muddy/sandy areas of the Sandy Hook peninsula (NJ) in July 2005. We also collected around 300 specimens of *Ilyanassa obsoleta*, the dominant gastropod species in the area, the shell of which is most often used by the Sandy Hook population of *P. longicarpus*. Shell length (SL) (estimated from the shell base–apex axis) ranged between 9 and 21.9 mm. All the measures were taken using vernier calipers (accuracy: 0.05 mm).

After the capture, the crabs were immediately transferred to the laboratory at Peekskill (NY), where they were held in 20-l aquaria with aerated artificial seawater (Instant Ocean salts) at the same salinity as natural seawater (27 ppt). They were maintained in a temperature-controlled room (24 °C) under

a natural 14:10 light:dark cycle and fed a diet of commercial shrimp pellets every day. The water was changed every second day.

The optimal length of shells for crabs of a given size was determined from the regression line $y = 3.48x + 8.65$, where y is SL and x is CW, both in millimeters. This equation was obtained from a preliminary free-choice experiment in which 30 crabs (CW: 0.1–0.3 mm) were separately allowed to choose among 3 empty undamaged and unfouled *I. obsoleta* shells of different sizes (SL: 9–21.8 mm). The offered shells were prepared by boiling live gastropods and removing the flesh, rinsing the shells several times in alcohol and seawater, and air-drying them. Shells with a length 10% greater, or 10% less, than the optimal shell (OS) for a given crab were defined as larger shell (LS) or smaller shell (SS) than OS. Previous studies (e.g., Gherardi 2006) had shown that these 3 relative sizes meet the criterion of optimality/suboptimality of shells for *P. longicarpus*. Crabs occupying OS, LS, and SS will be hereafter abbreviated as OC, LC, and SC, respectively.

General methods

Experiments were staged in opaque plastic bowls (diameter: 10 cm), containing 160 ml unfiltered 27-ppt standing seawater at 22 °C, and illuminated during observations by a 75-W incandescent light, 50 cm above the water level. Observations were always conducted between 9 and 18 h. Sex was not noted because sex has been shown to exert no effect on agonistic interactions in this and other hermit crab species (Hazlett 1966a; Winston and Jacobson 1978), at least during the non-reproductive period (in New England, this species reproduces between October and May with a peak in the autumn; Wilber 1989). After being used in the experiments, crabs were released at the collection site.

Experimental design

Sixty hermit crabs were randomly assigned to one of 3 groups that differed in the quality of the occupied shell, that is, 20 OC, 20 LC, and 20 SC. These 3 groups were obtained by forcing individuals (the original shells of which were gently broken with a vice) to occupy new unfouled and undamaged *I. obsoleta* shells of differing quality, prepared as described above. Crabs were then allowed 2 days to acclimatize to the new condition.

Following Gherardi and Tiedemann (2004b), we assessed the intensity of crabs' motivation for shell switching from the behavior that individuals displayed toward an empty novel shell offered to them in a noncompetitive context. Snail odor was used to make the offered shell attractive for them. In fact, previous studies had shown that *P. longicarpus*, in both adequate and inadequate shells, responds to an empty shell only when its sight is accompanied with chemical cues (Gherardi and Atema 2005) and that, both in the laboratory and in field, extracts of snail flesh are more attractive than the odor of dead or live conspecifics (Gherardi and Atema 2005, Tricarico and Gherardi 2006).

So, the experimental bowl was provided with an empty shell of different quality for the test crab (OS, LS, or SS), placed with its apex upward. To avoid its occupancy by the crab, the shell had its aperture blocked with a resin, which preliminary observations had shown to have no effect on shell attractiveness. The bowl also contained 3 ml of snail solution diluted in 160 ml of seawater. To generate stock solutions of snail flesh, we incubated (and then filtered following Rittschof 1980a, 1980b) frozen and then thawed pieces of *I. obsoleta* flesh in seawater for 1 h at room temperature in the ratio of 3 g (ca. 2 g dry weight) flesh/100 cc seawater (Gherardi and Atema 2005).

Each crab (OC, SC, or LC) was offered 3 novel shells of differing quality (OS, LS, and SS), one per day, during 3 consecutive days. The sequence of the shells offered was varied systematically per crab. Between observations, crabs were maintained in their individual bowl and fed with 0.5 g of dried shrimp pellets to keep them satiated.

Observations started with the insertion of an individual into the bowl at about 8 cm from the shell. During the 10-min observations, we recorded on a voice tape the behavior of the test crab to obtain 1) latency in seconds (time until the first shell investigation; when the test crab never investigated the shell, a time equal to 605 s was arbitrarily assigned), 2) number of shell investigations, 3) duration of the first shell investigation in seconds, and 4) total duration of shell investigations in seconds. For shell investigation, we mean the active exploration as described by Jackson and Elwood (1989b), particularly the external exploration (moving chelipeds over exterior of shell) and the aperture exploration (inserting one or more appendages into partially blocked aperture). To assess whether the intensity of test crabs' motivation to obtain the offered shell varied with time in response to the increased information gathered of the shell quality, we arbitrarily divided the 10 min of observation into 4 temporal phases of 2 min and 30 s each. For each of them, we recorded the number and total duration of shell investigation.

Data analyses

Statistical analyses were performed following the procedures found in Zar (1984). All data were checked for homogeneity of variance using the Levene test. To correct temporal autocorrelations arising from measurements repeated in time and to prevent pseudoreplication, data were subject to a 2- or a 3-way repeated measures analysis of variance (ANOVA) (statistic: F), where the quality of the offered shell was a repeated measure. Where significant F ratios were calculated by ANOVA, Student–Newman–Keuls multiple comparisons test (SNK) was applied to identify which data sets were different. Figures give mean values (and standard error). The level of significance at which the null hypothesis was rejected is $\alpha = 0.05$. From the analyses, we discarded the crabs that remained motionless for at least one trial, so sample sizes were 16 for OC, 16 for LC, and 18 for SC.

RESULTS

Latency was significantly shorter for SC than for OC and LC ($F = 6.18$, degrees of freedom [df] = 2,47, $P = 0.004$; after SNK: OC = LC > SC), being, however, independent of the quality of the offered shell ($F = 1.22$, df = 2,47, $P = 0.30$; interaction: $F = 1.21$, df = 4,94, $P = 0.31$) (Figure 1A). The number of shell investigation differed only among the groups of crabs ($F = 4.77$, df = 2,47, $P = 0.01$; after SNK: SC > OC = LC) but not among the qualities of the offered shell ($F = 0.88$, df = 2,47, $P = 0.42$; interaction: $F = 0.80$, df = 4,94, $P = 0.53$) (Figure 1B). As compared with OC and SC (after SNK: LC > SC > OC), LC investigated the offered shell for a longer time either in the first investigation ($F = 29.98$, df = 2,47, $P = 0.03$) or in all the investigations ($F = 5.76$, df = 2,47, $P = 0.006$), independently of its quality (duration of first investigation: $F = 0.39$, df = 2,47, $P = 0.68$; interaction: $F = 0.44$, df = 4,94, $P = 0.78$; total duration of investigation: $F = 0.41$, df = 2,47, $P = 0.67$; interaction: $F = 0.42$, df = 4,94, $P = 0.79$) (Figure 1C).

A 3-way ANOVA applied on the shell investigation did not show significant differences for both number and the total duration among groups of crabs, qualities of the offered shell, and temporal phases (number: $F = 1.30$, df = 4,535, $P = 0.27$; duration: $F = 0.57$, df = 4,535, $P = 0.69$). Only in the case of

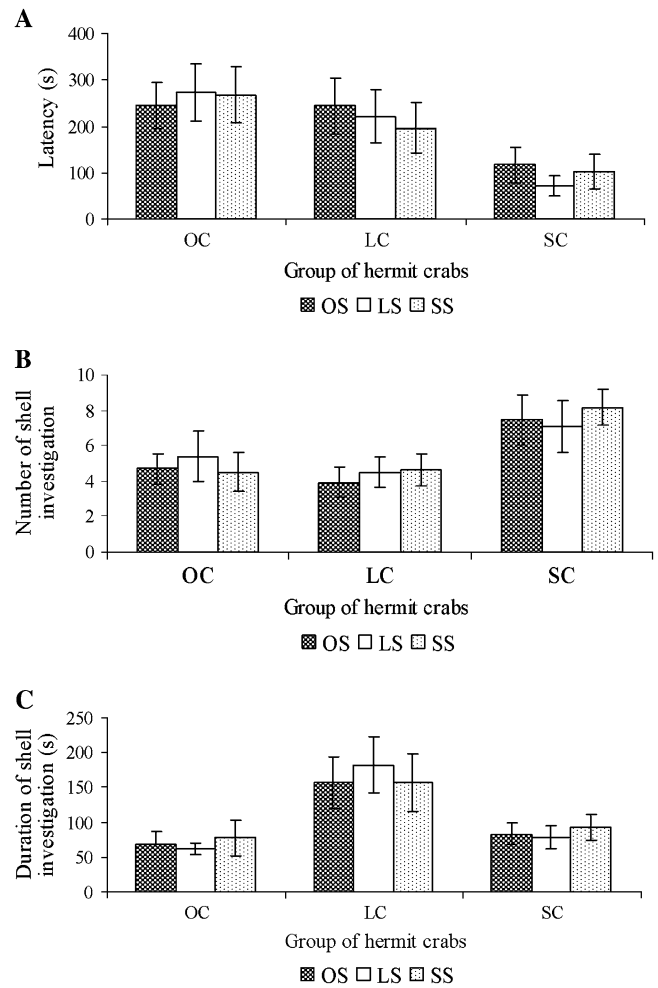


Figure 1

Mean (\pm standard error) (A) latency (in seconds) to approach an offered empty shell, (B) number of shell investigation, and (C) duration (in seconds) of shell investigation by crabs occupying an OS (OC, $n = 16$), a larger than OS (LC, $n = 16$), and a smaller than OS (SC, $n = 18$). The offered shell was optimal (OS), larger than optimal (LS), or smaller than optimal (SS).

SC did the number of shell investigation and its total duration significantly decrease with time, whereas no significant difference was found for both OC and LC (Table 1, number and duration of shell investigation).

DISCUSSION

The results of this study are clear in showing that *P. longicarpus*' motivation to acquire a new shell is strongly affected by the value of the shell it inhabits rather than by the quality of the shell it is offered with (ERV). In fact, hermit crabs' readiness to approach the offered shell and the extent of its investigation were independent of its quality but seemed to be related exclusively to their ORV.

Hermit crabs occupying small shells were more rapid in approaching the offered shell, whatever its quality was, than crabs in LSs or OSs. This result confirms Dowds and Elwood (1983) and Gherardi (2006), who suggested that individuals in suboptimal shells were highly motivated to initiate fights and, while fighting, persist longer. Additionally, crabs inhabiting shells of a small size or in poor conditions were most easily attracted to gastropod predation sites (Rittschof et al. 1995).

Table 1

Number and duration of shell investigation for crabs occupying an OS (OC, $n = 16$), a larger than OS (LC, $n = 16$), and a smaller than OS (SC, $n = 18$): comparisons among the 3 offered shells (OS, LS, or SS) within the 4 temporal phases using a 2-way repeated measures ANOVA (statistic: F) followed by SNK. Significant values in bold

	Phases				Offered shells				Phases \times offered shells		
	F	df	P	Hierarchy	F	df	P	Hierarchy	F	df	P
Number of shell investigation											
OC	0.67	3	0.41	1 = 2 = 3 = 4	0.61	2	0.54	OS = LS = SS	0.69	2	0.50
SC	6.96	3	0.009	1 = 2 > 3 > 4	1.30	2	0.27	OS = LS = SS	1.93	2	0.15
LC	0.35	3	0.55	1 = 2 = 3 = 4	0.50	2	0.61	OS = LS = SS	0.17	2	0.84
Duration of shell investigation											
OC	2.70	3	0.10	1 = 2 = 3 = 4	2.63	2	0.08	OS = LS = SS	0.44	2	0.64
SC	4.70	3	0.03	1 = 2 > 3 = 4	2.97	2	0.06	OS = LS = SS	1.41	2	0.25
LC	0.64	3	0.43	1 = 2 = 3 = 4	0.52	2	0.59	OS = LS = SS	0.21	2	0.81

Similarly, in the house crickets, *Acheta domesticus*, a restricted prior access to mates was found to increase the rate at which males initiated and escalated fights (Brown et al. 2006), and a differential prior exposure to food led to motivational asymmetries in which hungry crickets won more fights over the possession of food (Nosil 2002). The readiness of an animal to either attack a conspecific or investigate a resource denotes its motivation to fight or to acquire that resource, as found by Enquist and Jakobsson (1986) in the cichlid fish, *Nannacara anomala*. Enquist and Leimar (1987) reviewed several studies conducted in different species and showed a relationship between the value of the contested resource and the agonistic behavior. Both fight duration and the frequency of potentially dangerous behavioral patterns increase with augmented resource value, such as food (in the hermit crab *Calcinus tibicen*, the spider crab *Microphrys bicornutus*, the crayfish *Orconectes rusticus*, the house cat *Felix catus*, and the chimpanzee *Pan troglodytes*; references in Enquist and Leimar 1987). Specifically, when the resource value increases for 1 of the 2 contestants, without any parallel increase in the opponent, that individual is likely to win more often as predicted by the model of owner-intruder conflicts with information asymmetry (e.g., in female iguanas or in male spiders competing for nesting burrows or for females, respectively; Rand WM and Rand AS 1976; Austad 1983; Bridge et al. 2000). Besides, crabs in shells smaller than optimal investigated more often the offered shell, whatever its quality was, possibly because crabs occupying small shells, being less fatigued, are more active.

Contrary to our expectations, crabs in LSs were found to investigate the offered shell, regardless of the latter's quality, for longer than SC. LSs provide protection against predators and, being heavier, allow them to avoid dislodgement from the substrate in a high-flow environment (Hahn 1998). Nevertheless, they may impose large energetic costs for carrying (Elwood 1995), especially in still water, and thus decrease crab fitness and increase crab motivation to find better shells. They seem also to affect reproduction, as shown in 3 tropical hermit crab species, in which shells were heavier in nonovigerous than in ovigerous females (Bertness 1981a).

Only in SC did we find a decrease in the frequency and duration of shell investigation with time: individuals in urgent need of a new domicile may waste time and energy, and risk being exposed to predators, in their attempts to occupy an inaccessible resource. This result agrees with Elwood (1995), who showed that crabs housed in shells 50% lighter than the optimum weight, once offered with an OS with the blocked aperture, had a longer startle response after having investigated the blocked aperture for 10 s than after having con-

tacted the shell and the aperture for 3 and 2 s, respectively. On the contrary, Kinoshita and Okajima (1968) recorded naked crabs or crabs in small shells persisting for longer periods of time to explore high-quality shells with blocked apertures than did crabs in good shells, as a possible consequence of their elevated motivation state.

Contrary to SC, the frequency and duration of shell investigation did not significantly change with time in LC and OC. Possibly, crabs are unable to acquire information about ERV or, if they are able to do that, they are not using such information. In contrast, Neil and Elwood (1986) found that, whereas *P. bernhardus* rejected shells with blocked apertures, they did so more quickly when offered shells of suboptimal, rather than optimal, size. Some fish and finch species were previously found to neglect information gathered during resource assessment, at least in the agonistic context. Neat et al. (1998) and Maan et al. (2001) observed that in the cichlid *Tilapia zillii* and *Aequidens rivulatus*, fish smaller than their opponents often continued to fight, in spite of information about their size disadvantage, and frequently won fights. A similar behavior was recorded in the subordinate finches *Serinus serinus* when they overcome dominants in disputes over food (Senar et al. 1992).

Our study confirms what previously suggested by Gherardi (2006) that ORV affects *P. longicarpus*' motivation to explore and fight for a novel shell and that this species does not gather—or does not use—information about shell quality during investigation. Our results contrast with Elwood and Neil (1992), Elwood (1995), and Briffa and Elwood (2001), who showed that *P. bernhardus* is subject to motivational changes during shell fights as the result of the acquired information about the resource at stake, mainly basing its strategic decisions on a fine comparison between the quality of the domicile shell and the quality of the offered shell.

Indeed, *P. longicarpus* is inaccurate in distinguishing shells by sight alone (Gherardi and Tiedeman 2004a, 2004b), most often switching shells without prior investigation (Scully 1986). Shell investigation in this species is a rare event, and in the few instances when it occurs, it simply consists of a quick inspection of the outer surface of the shell (Gherardi 2006). While fighting, *P. longicarpus* attacks any individual of the group, independently of the defender's resource value, and the duration of its fight seems to be unrelated to the different quality of the shell at stake. Shell fights and spasmodic shakings are also rare events in natural conditions within the aggregations formed in gastropod predation sites (Tricarico and Gherardi 2006), which seemed not to function as shell exchange markets as suggested for other species

(e.g., *Calcinus laevis*, Gherardi and Vannini 1993; *Clibanarius erythropus*, Gherardi and Benvenuto 2001). It is likely that the diverse hermit crab species differ in the sensory modalities they use to assess the quality of the shell at stake. Whereas *P. bernhardus* adopts visual and tactile cues (Elwood and Stewart 1985) and *C. vittatus* is able to gather information about ORV and ERV when it negotiates shells (Hazlett 1996), *P. longicarpus* may assess the quality of an external shell only after having worn it, as found also in *Clibanarius tricolor* (Bach et al. 1976) and *C. vittatus* (Diaz et al. 1994, 1995). In fact, immediately upon its arrival at a gastropod predation site, *P. longicarpus* quickly enters the empty shell found without abandoning its domicile shell until it has tried the new one (Tricarico and Gherardi 2006). It seems therefore likely that, under a physiological point of view, the decision to keep the novel shell or to return to the old one requires some proprioceptive information that the crab is able to acquire only by wearing it, a hypothesis that certainly deserves further studies.

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