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The past ownership of a resource affects the agonistic behavior of hermit crabs

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Abstract Resource value is often considered the most important nonstrategic variable in the fighting behavior of invertebrates. In our study, we tested whether the experience of shells of a given quality, occupied in the recent past, might affect the agonistic behavior of the hermit crab *Pagurus longicarpus*. We analyzed the fights battled by 84 test crabs against size-matched unknown rivals before (premanipulation phase) and after (postmanipulation phase) having modified the quality of the domicile shell of the contestants. Specifically, we compared the behavior of crabs that had been subject to either a worsening or an improvement in the quality of their shell with crabs that, although being similarly subject to a shell manipulation, occupied a shell of the same quality as in the premanipulation phase. We found that the crabs subject to a worsening in the quality of their shell were more aggressive than those subject to its improvement and that the former were even more aggressive than those that occupied a bad quality shell also in the premanipulation phase. Crabs seemed not to gather information about the opponent's shell during fights or not to use this information, most often behaving in accordance with the quality of the domicile shell. These results are clear in showing the role played by the experience of a previously occupied shell, also confirming that the agonistic behavior of *P. longicarpus* is mainly based on decision rules of the type "own resource value dependency."

Introduction

According to several strategic models of aggression available in the literature, the degree of escalation of a contest and its outcome can be easily predicted from asymmetries in one of three types of traits characterizing the contestants: resource holding power (RHP), relative resource value (RV), and aggressiveness (e.g., Maynard Smith and Parker 1976; Enquist and Leimar 1983, 1987; Hurd 2006). RHP is the ability to win a contest, is typically related to body and/or weapon size (Parker 1974; Maynard Smith 1982), and can also be subject to intersexual variation (Briffa and Dallaway 2007); RV refers to the gain of having exclusive access to the contested resource, which may vary among individuals (Maynard Smith 1982), while aggressiveness is an inherent property of the individual (Barlow et al. 1986), which seems unlikely to occur independently of the other two traits (Hurd 2006). All three of these factors taken together affect the choice of whether or not to escalate a fight and when.

The importance of RV has been investigated in a variety of taxa (reviewed in Enquist and Leimar 1987). The higher the value of the resource at stake, the more risks the contestant will take to gain possession of it. Indeed, resources that yield adaptive advantages to the owner evoke escalated combats in several species (e.g., in hummingbirds; Dearborn 1998, in honey bees; Gilley 2001, but not in the fallow deer (Jennings et al. 2004)), compared with resources that slightly influence fitness (e.g., patches of sunlight in *Pararge aegeria*, Davies 1978). Often, a high aggressiveness might help individuals

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overcome inferior RHP (e.g., Sigurjónsdóttir and Parker 1981; Austad 1983; Barnard and Brown 1984; Ewald 1985; Verrell 1986; Yokel 1989; Haley 1994; Neat et al. 1998; Kotiaho et al. 1999; Gherardi 2006).

The value of the contested resource varies across individuals as a reflection of their diverse perception of it (Enquist and Leimar 1987): it may depend on the physiological state of an animal (e.g., hunger in several crustacean decapods; Hazlett et al. 1975) and on the accuracy of the information gained about that resource and/or about its availability in space and time (e.g., nesting burrows in female iguanas; Rand and Rand 1976). For instance, shelters have a greater value for maternal rather than nonmaternal females of the American lobster, *Homarus americanus* (Figler et al. 1998): the former, which have more to gain, are more likely to escalate and win combats for access to them. Funnel-web spiders (*Agelenopsis aperta*) fight longer during territorial disputes when suitable web sites are in short supply than when these are abundant (Riechert 1978). Copulating spider (*Frontinella pyramitela*) males get information on how many eggs remain to be fertilized from the time they have been mating with a female and adjust their behavior accordingly if attacked by an intruder (Austad 1983). Subjective resource value may also derive by how extensively the owner has invested on a given resource, being more willing to take risks for its defense when the costs faced for its recruitment and maintenance have been high (e.g., the nest in the European robin and in sand gobies; Tobias 1997; Lindström and Pampoulie 2005).

Hermit crabs have been traditionally used as model organisms to study the dynamics of resource fighting. Gastropod shells are vital resources for most of them (for exceptions, see Gherardi 1996a), providing protection from predators (Hazlett 1981), dehydration, temperature extremes (Taylor 1981), salinity changes (Davenport et al. 1980), and predatory pressure (Vance 1972). However, not all the domicile shells are equal for the crab. A shell that is too small will inhibit growth (e.g., Angel 2000), reduce protection against predators (e.g., Angel 2000), and lower survival (e.g., Borjesson and Szelistowski 1989) and reproductive success in both males (Hazlett 1989) and females (e.g., Elwood et al. 1995). On the other hand, a shell that is too large makes locomotion energetically wasteful (in terrestrial hermit crabs, Herreid and Full 1986) and has negative effects on female reproduction (Fotheringham 1980). As a consequence, there is a strong selective pressure for the crabs to obtain a shell of the appropriate size.

Fights for shell ownership are common (for a complete description, see Elwood and Briffa 2001). In a typical fight, the attacker approaches and grasps the shell of the defender, causing the latter to withdraw into its shell. The attacker climbs over the exterior of the defender's shell, turns the shell, and feels into the aperture with its chelipeds or with other appendages. The attacker may escalate the contest by repeatedly rapping (in diogenids) or shacking (in pagurids) the two shells together in discrete bouts, interspersed with pulling the defender's chelipeds (Hazlett 1966). This may cause the defender to either spontaneously leave the shell or release its abdominal grip on the shell, thus being pulled out by the attacker, allowing the latter to take the defender's shell. Alternatively, the attacker may give up the fight at any stage.

Most studies on the dynamics of shell fighting have followed the predictions of classic game theory models (e.g., Parker and Rubenstein 1981; Enquist and Leimar 1983, 1987), denoting the ability of crabs to assess, along with the RHP of their opponent (Briffa and Elwood 2000a, b), the quality of the rival's shell relative to that of its own (Elwood and Neil 1992; Hazlett 1996a; Wada et al. 1997). The subjective value of the occupied shell may induce a crab to attack, but its subsequent decision whether to escalate or to retreat was found to depend upon the estimated increase in shell quality the attacker may gain (Dowds and Elwood 1983). Shell fighting has been thus viewed as a process of information gathering that may alter the perceived value of the contested resource, causing the motivational state for fighting to vary (Jackson and Elwood 1989; Briffa and Elwood 2001).

Only recently was the hypothesis raised that shell fighting in hermit crabs might follow decision rules of the type 'own RV-dependent persistency': an individual seems to decide whether to persist or to withdraw in accordance with its own resource value (Gherardi 2006) and not on the basis of the estimated gain in resource quality. This is possibly the consequence of some hermit crab species' inadequate sensory acuity, high costs of assessment, or lack of reliable cues in certain habitats (Taylor and Elwood 2003). It was also suggested that the agonistic behavior of hermit crabs is affected by the experience they may have had of shells of a given quality (Gherardi 2006). Such alternatives to the traditional views of the dynamics of resource fighting have many obvious implications in studies on hermit crabs and other organisms but, to the best of our knowledge, have received little attention in the literature.

In this study, we will examine in *Pagurus longicarpus* as a model organism the hypothesis that the decisions made by individual crabs during shell fighting might be influenced not only by the RV of the presently occupied shell but also by the quality of the shell it occupied in the recent past. Therefore, we investigated the agonistic behavior displayed by test crabs toward a size-matched unknown rival before and after having modified the quality of their domicile shell. Specifically, individuals that had been subject to a change in their own RV were compared in their agonistic

behavior with those that had acquired a resource of the same value as that before shell manipulation.

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 USA and in the Gulf of Mexico (Williams 1984). Around 400 specimens with a major chela width (CW) of 0.1–0.5 mm were collected from muddy/sandy areas of the Sandy Hook peninsula (New Jersey, USA) in July of 2005. We also collected around 300 specimens of *Ilyanassa obsoleta*, the dominant gastropod species in the area whose shell 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 measurements were taken using vernier calipers (accuracy= 0.05 mm).

After the capture, the crabs were immediately transferred to the laboratory at Peekskill (New York, USA), where they were held in 20-l aquaria with aerated artificial seawater (Instant Ocean™ salts) with the same salinity as natural seawater (27 ppt). They were maintained in a temperature-controlled room (24°C) under a natural 14-h light/10-h dark cycle and fed a diet of commercial shrimp pellets every day. The water was changed every other day.

The optimal shell length (ranging between 14.5 and 20.0 mm) 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 (Tricarico and Gherardi 2007). Shells with a length 10% (±1%) less than the optimal shell for a given crab were defined as suboptimal shells. Crabs occupying optimal and suboptimal shells will be hereafter abbreviated in O and S, respectively.

General methods

Experiments were staged in opaque plastic bowls (diameter= 10 cm), containing 160 ml unfiltered standing seawater (salinity=27 ppt) at 22°C, illuminated during observations by a 75-W incandescent light 50 cm above the water level. Observations were always conducted between 09:00 and 18:00 hours. Sex was not noted because sex has been shown to exert no effect on agonistic interactions in this and other hermit crab species (Winston and Jacobson 1978) during the nonreproductive 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

Ninety-two crabs were randomly assigned to one of two groups that differed for the quality of the occupied shell (i.e., 46 O and 46 S). These two groups were obtained by forcing individuals (the original shells of which were gently broken with a vice) to occupy an optimal or a smaller than optimal shell.

Test crabs were left in their individual bowl for 24 h before the experiment started. Crab size was equal in the two groups ($t=1.55$, $df=90$, $p=0.13$; mean major chela size= 2.43±0.06 mm). The experiment was composed of two phases: the first preceding (premanipulation phase) and the second after (postmanipulation phase) shell manipulation. In the premanipulation phase, test crabs (either O or S) were kept for 5 min in the presence of a size-matched, unknown rival occupying an optimal shell. Rival crabs were used only once. In the postmanipulation phase, crabs that had not switched their shell with the previous rival in the premanipulation phase (three pairs switched their shells) or that did not die during the shell manipulation (five crabs died) were forced to enter a novel shell to obtain four groups: (1) 21 formerly O occupying again an optimal shell (OO), (2) 21 formerly S occupying again a suboptimal shell (SS), (3) 21 formerly O occupying a suboptimal shell (OS), and (4) the remaining 21 formerly S occupying an optimal shell (SO). Test crabs were then kept in their individual bowl for 24 h before being subject to the postmanipulation phase, in which each of them was again kept for 5 min in the presence of a novel rival crab as above.

Both pre- and postmanipulation phases started by simultaneously placing the test crab and the rival into the experimental bowl in the opposite sides. During each trial, we recorded the behavior of test crabs on a voice tape to obtain: (1) latency (time until the first attack by the test crab in seconds), (2) number of attacks by the test crab, (3) percentage of shell fights (investigation, spasmodic shaking, jumps over) initiated by the test crab on the total number of fights, (4) total duration of the shell fights initiated by the test crab, (5) numbers of shell investigation, spasmodic shaking, strong contacts (grasps and strikes), and jumps over the rival performed by the test crab (Gherardi and Tiedemann 2004), and (6) number of shell fights, attacks, and strong contacts through the time. Spasmodic shaking is a typical behavior that pagurids execute during shell fights, analogous to shell rapping of the diogenids (Hazlett 1966); it consists of rapid back-and-forth movements of the defender's shell by the attacker's pereopods. Jumps over show a high aggressiveness in the attackers; the behavior consists of the crabs moving toward the opponents and quickly jump on the opponents' shell. Immediately after this attack, the crabs usually execute shell investigation or, more often, spasmodic shaking.

To assess whether test crabs can modulate their agonistic behavior with time in accordance with the increased information gathered during interactions, we divided the 5 min of every trial in five temporal bouts of 1 min each and analyzed the number of shell fights, attacks, and strong contacts through time. We also recorded the number of defenders, if any, evicting from their shell. Between observations, crabs were maintained in their individual bowl and fed with 0.5 g of dried shrimp pellets to keep them satiated.

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, and data were normalized using arcsine square root transformation (i.e., percentage of shell fights). To correct temporal autocorrelations arising from measurements repeated in time and to prevent pseudoreplication, data of all the recorded parameters were subject to a two-way repeated measures analysis of variance (ANOVA; statistic, F, the two factors were crab groups and temporal phases), where individual crabs were repeated measures. To compare the four groups of crabs separately in the pre- and in the postmanipulation phases, we used an one-way ANOVA (statistic, F). Where significant F ratios were obtained by both ANOVAs, Student Newman–Keuls Multiple Comparisons test (SNK) was applied to identify which data sets were different, α levels being corrected by a Bonferroni correction to reduce type-I error. Each group of crabs in the pre- and postmanipulation phases was compared using a paired samples Student's t test (statistic, t). To assess whether the number of shell fights, attacks, and strong contacts decreased with time, we used a Spearman rank-order correlation (statistic, r_s).

From the analyses, we discarded the individuals that remained motionless for at least one trial, so sample sizes were 19 for OO and 20 for OS, SS, and SO. From the analysis of latency, we also discarded test crabs that never attacked the rival; therefore, sample sizes were 17 for OO, 16 for OS, 19 for SS, and 18 for SO in the premanipulation phase and 15 for OO, 16 for SO, and 20 for OS and SS in the postmanipulation phase.

The level of significance at which the null hypothesis was rejected is $\alpha=0.05$ ($\alpha=0.0125$ after Bonferroni correction).

Results

In the premanipulation phase, OS were similar to OO and SO to SS for all the recorded parameters (Tables 1 and 2). In the postmanipulation phase, OS displayed a more intense

Table 1 Mean values (SE in parentheses) of the recorded parameters before (pre) and after (post) shell manipulation

	OS				OO				SO				SS			
	Pre		Post		Pre		Post		Pre		Post		Pre		Post	
	M	SE	M	SE	M	SE	M	SE	M	SE	M	SE	M	SE	M	SE
Latency (s)	128.65	19.49	37.13	8.59	123.57	20.91	109.14	17.82	35.08	6.92	68.61	17.47	54.83	11.35	49.22	12.50
Attacks	2.55	0.57	5.65	0.67	2.00	0.45	2.52	0.41	4.85	0.97	3.15	2.60	5.30	1.21	3.10	0.35
Shell fights (%)	34.78	8.12	70.52	7.40	38.45	10.52	35.17	11.90	60.15	9.34	40.29	8.11	63.52	8.29	54.00	8.78
Duration shell fights (s)	35.80	10.11	117.35	23.72	30.26	4.75	24.21	6.55	65.90	15.68	36.15	12.73	73.45	18.81	71.45	19.92
Spasmodic shakings	0.10	0.07	0.65	0.17	0.00	0.00	0.10	0.07	0.30	0.11	0.05	0.05	0.30	0.18	0.50	0.14
Shell investigations	0.20	0.12	1.60	0.27	0.16	0.09	0.42	0.16	0.80	0.16	0.40	0.13	0.80	0.25	0.65	0.26
Jumps over	0.00	0.00	0.70	0.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.03
Strong contacts	0.25	0.10	1.90	0.39	0.68	0.23	0.42	0.19	1.65	0.22	0.34	0.18	1.80	0.21	1.10	0.33

OO Crabs occupying optimal shells in both pre- and postmanipulation phases, *OS* crabs occupying optimal shells in the premanipulation phase and suboptimal shells in the postmanipulation phase, *SO* crabs occupying suboptimal shells in the premanipulation phase and optimal shells in the postmanipulation phase, *SS* crabs occupying suboptimal shells in both pre- and postmanipulation phases

Table 2 Comparisons among the four groups of hermit crabs (OO: $n=19$; OS, SO, SS: $n=20$) in the pre- and postmanipulation phases after one-way ANOVAs (statistic, F), followed by SNK; df is 3, 65 for the latency in premanipulation phase, df is 3, 66 for latency in postmanipulation, and df is always 3, 75 for the all the other parameters

	Premanipulation phase			Postmanipulation phase		
	F	p	Hierarchy	F	p	Hierarchy
Latency (s)	4.86	*0.004*	OO=OS>SS=SO	3.78	*0.01*	OS=SS>SO=OO
Attacks	3.59	*0.010*	SS=SO>OO=OS	7.12	*<0.001*	OS>SS=SO>OO
Shell fights (%)	3.65	*0.010*	SS=SO>OO=OS	3.59	*0.01*	OS>SS>SO=OO
Duration shell fights (s)	3.80	*0.010*	SS=SO>OO=OS	5.87	*0.001*	OS=SS>SO=OO
Spasmodic shakings	4.30	*0.007*	SS=SO>OO=OS	3.97	*0.009*	OS>SS=SO>OO
Shell investigations	4.79	*0.004*	SS=SO>OO=OS	3.50	*0.01*	OS>SS>SO=OO
Jumps over	/	/	/	21.12	*<0.001*	OS>SS=SO=OO
Strong contacts	13.59	*<0.001*	SS=SO>OO=OS	5.97	*0.001*	OS>SS>SO=OO

Significant differences of ANOVA in italics. No jumps over were ever recorded in the premanipulation phase. See Table 1 for the meaning of OS, OO, SO, and SS.

agonistic behavior (Table 2). They executed a larger number of attacks, strong contacts, spasmodic shakings, jumps over, and shell investigations than SS, whereas they were as ready to attack the rival as SS and fought for a long time as the latter (Table 2). SS were more often the second most aggressive crabs (Table 2), whereas SO, even if significantly less aggressive than SS, did not behave as OO for all the parameters (Tables 2 and 4). All the analyzed parameters showed that the agonistic behavior of OS was significantly stronger in the post- than in the premanipulation phase (Table 4). On the contrary, SO were less ready to attack and executed less strong contacts and shell investigations in the postmanipulation phase; no significant differences were found for the other parameters (Table 4). OO and SS showed no significant difference in their agonistic behavior in the pre- and postmanipulation phases (Table 4). A two-way repeated measures ANOVA showed a significant interaction between the crab group and the two phases for all the recorded parameters (Table 3).

No significant decrease with time was found in all the groups of crabs, both in the pre- and postmanipulation phases, for the numbers of shell fights (r_s between −0.08 and 0.04, n between 95 and 100; p between 0.46 and 0.68), attacks (r_s between −0.01 and 0.05, n between 95 and 100; p between 0.65 and 0.95), and strong contacts (r_s between −0.02 and −0.19, n between 95 and 100; p between 0.07 and 0.85). No jumps over were ever recorded in the premanipulation phase.

Discussion

Our results clearly show that the experience of a previously occupied shell strongly affects and alters the agonistic behavior of *P. longicarpus*, pointing out for the first time that a change in the perceived resource value may be more important than the perceived value resource itself. Moreover, this species seems not to gather—or to use—information

Table 3 Comparisons between pre- and postmanipulation phases and among the four groups of hermit crabs (OO: $n=19$; OS, SO, SS: $n=20$) after two-way repeated measures ANOVAs (statistic, F), followed by SNK or t test

	Pre-/Postmanipulation phases, Within subjects				Crab groups, Between subjects				Phases × Crab groups, Interaction		
	F	df	p	Hierarchy	F	df	p	Hierarchy	F	df	p
Latency (s)	1.33	1, 137	0.25	pre=post	5.26	3, 135	*0.001*	OS=SS>SO>OO	2.57	3, 134	*0.05*
Attacks	0.02	1, 156	0.88	pre=post	3.17	3, 154	*0.02*	OS=SS=SO>OO	5.84	3, 149	*<0.001*
Shell fights (%)	3.74	1, 156	*0.05*	pre<post	1.30	3, 154	0.28	OS=SS=SO=OO	4.97	3, 149	*0.002*
Duration shell fights (s)	0.47	1, 156	0.50	pre=post	5.05	3, 154	*0.002*	OS=SS>SO=OO	5.78	3, 149	*<0.001*
Spasmodic shakings	18.62	1, 156	*<0.001*	pre<post	5.00	3, 154	*0.002*	OS>SS>SO>OO	2.91	3, 149	*0.04*
Shell investigations	4.31	1, 156	*0.04*	pre<post	3.77	3, 154	*0.01*	OS>SS=SO>OO	8.93	3, 149	*<0.001*
Strong contacts	0.43	1, 156	0.51	pre=post	4.64	3, 154	*0.004*	OS=SS>SO>OO	12.78	3, 149	*<0.001*

Significant differences of ANOVA in italics. No jumps over were ever recorded in the premanipulation phase. See Table 1 for the meaning of OS, OO, SO, and SS.

Table 4 Comparisons between the pre- and postmanipulation phases for each group of crabs (OO: $n=19$; OS, SO, SS: $n=20$) after paired t tests (statistic, t)

	OS			OO			SO			SS		
	t	p	Hierarchy	t	p	Hierarchy	t	p	Hierarchy	t	p	Hierarchy
Latency (s)	3.64	0.002	pre>post	1.33	0.21	pre=post	−2.25	0.04	pre<post	0.31	0.76	pre=post
Attacks	−3.40	0.003	pre<post	−1.10	0.29	pre=post	1.43	0.17	pre=post	1.64	0.12	pre=post
Shell fights (%)	−5.03	<0.001	pre<post	−1.00	0.33	pre=post	0.57	0.58	pre=post	0.99	0.33	pre=post
Duration shell fights (s)	−3.71	0.001	pre<post	0.68	0.51	pre=post	1.59	0.13	pre=post	0.52	0.61	pre=post
Spasmodic shakings	−2.98	0.008	pre<post	−1.46	0.16	pre=post	−2.03	0.06	pre=post	−1.29	0.21	pre=post
Shell investigations	−5.27	<0.001	pre<post	−1.32	0.21	pre=post	2.18	0.04	pre>post	0.43	0.67	pre=post
Strong contacts	−4.28	<0.001	pre<post	0.87	0.40	pre=post	4.52	<0.001	pre>post	1.85	0.08	pre=post

For latency, df is 13 for OO and SO, 15 for OS, and 17 for SS. For the other parameters, df is 18 for OO and 19 for OS, SO, and SS. Significant values of t tests in italics. Jumps over were excluded from the analysis because they had been never recorded in the premanipulation phase. See Table 1 for the meaning of OS, OO, SO, and SS.

about the quality of the rival's shell as the fight proceeds and does not modulate its agonistic behavior accordingly, as on the contrary found by Elwood et al. 1998 and Briffa and Elwood 2001 in *P. bernhardus* (the numbers of shell fights, attacks, and strong contacts did not decrease with time).

Confirming previous observations (Gherardi 2006), this study suggests that crabs perceive a change in the value of the held resource and significantly modify their agonistic behavior after shell manipulation, as confirmed by the significant interactions obtained for all the parameters between crab groups and phases. Specifically, a worsening of the shell quality leads to a significant intensification of aggression (strong contacts, attacks, spasmodic shakings, and shell fights increase in number), and OS become even more ready to attack the opponent and to explore its shell than SS. They execute more numerous strong contacts, shell investigations, and spasmodic shakings than SS, and they jump over the rival more often as an expression of their strong aggressiveness. In accordance with Dowds and Elwood 1983 and Gherardi 2006, shell quality significantly influences the level of aggression in hermit crabs: crabs occupying suboptimal shells (OS and SS) are more ready to attack the rival and execute more numerous strong contacts and shell fights. Indeed, the more intense agonistic behavior recorded in hermit crabs occupying poor-quality shells is an adaptive strategy evolved to accommodate their individual growth, to protect them from predators, and to increase their reproductive success (Hazlett 1970a, b; Vance 1972; Bach et al. 1976; Hazlett 1978, 1980; Gherardi 1996b). Similarly, in the house crickets *Acheta domesticu*s, a differential prior exposure to food can cause motivational asymmetries among combatants, the hungry individuals being more aggressive and more likely the winner (Nosil 2002); in this species, males isolated from females for 4 days initiated aggression more often than males that were made free to encounter females during the four previous nights (Brown et al. 2006).

The worsening in the quality of the inhabited shell caused a stronger response than its improvement. In fact, OS drastically altered their fighting behavior after shell manipulation, but, unexpectedly, an improvement in the shell quality of SO was not sufficient in mitigating the intensity of their agonistic behavior. It induced only a significant decrease in the frequency of both strong contacts and shell investigations during the postmanipulation phase. In large part, the changes recorded in the behavior of OS and SO can be ascribed to the effect of prior experience with shells previously occupied and are not a consequence of the potential disturbance because of shell manipulation; in fact, those crabs that were not subject to a change in the quality of the inhabited shell (OO and SS) shared the same behavior in the pre- and postmanipulation phases.

Experience is known to play a relevant role in different aspects of behavior. Whitehouse (1997) and Stuart-Fox (2006) underlined that multiple traits and contextual factors might influence both the ability to combat and the outcomes of fights in several vertebrate and invertebrate species. The influence of past social experience, in the form of "winner and loser effects," can maintain dominance hierarchies ("confidence hierarchies," Goessmann et al. 2000): successful fighting experiences may make an animal more prone to escalate encounters and increase its perception of self or of its resource-holding power (Parker 1974). Experience may also reduce an animal's reliance on the assessment of its opponent's attributes (Whitehouse 1997). For example, in the spider *Misumenoides formosipes*, experience is used to evaluate its own fighting caliber and exercises a primary role in fighting behavior even when the assessment of both body size and residency status provide contrasting information (Hoefler 2002).

Prior experience with conspecifics or with resources, in concert with appropriate physiological conditions, can also influence an animal's reproductive behavior, as found in the walnut fly, *Rhagoletis juglandis* (Carsten and Papaj 2005),

or in the beetle *Callosobruchus maculates* (Yang et al. 2006). After the subordinates of the convict cichlid, *Cichlasoma nigrofasciatum*, were given the access to a mate, they were more persistent in fighting once met again by the dominants (Keeley and Grant 1993). In addition, foragers can increase their efficiency by modifying their behavior according to memories of past experience at particular sites (Ohashi and Thomson 2005).

From our results, we may hypothesize that aggressiveness in crabs varies with a change in the quality of the shell they occupy but that it is still affected by their previous conditions. It is known that changed contacts between the columella of the gastropod shell and the lateral surface of the crab abdomen are detected by mechanoreceptors, innervating the soft cuticle of the abdomen and controlling its stiffness (Chapple 2002). It may be possible that this mechanism alters the crabs' internal state, but the experience of a previous shell might induce a form of habituation in them and be remembered after a shell change. Indeed, a number of studies have shown that hermit crabs are able to remember shells (e.g., Hazlett 1992, 1996b). *Pagurus bernardus* recognizes previously investigated shells (but not their location; Jackson and Elwood 1989); *Pagurus acadianu*s, once removed from its shell and given a choice between its original shell and a novel one of the same size, prefers the former (Grant 1963). Gherardi (2004) found that the experience of inhabiting a given shelter (either a shell or a vermetid tube) predisposes *Calcinus tubularis* to choose the same type of domicile, a phenomenon that might allow for the maintenance in the study population of an intersexual displacement of shelters (males inhabit shells and females inhabit tubes). Nevertheless, to the best of our knowledge, no studies have ever proved that the experience of a previous shell might influence the agonistic behavior in hermit crabs and that the change in resource quality might be more important than the quality itself.

Finally, the present study confirms that *P. longicarpus* is unlikely to assess the quality of the rival's shell, as suggested by previous laboratory experiments in which this species showed to inaccurately distinguish shells by sight (Gherardi and Tiedemann 2004); hermit crabs often switched shells without prior investigation (Scully 1986), approaching any individual of the group, independent of the defender's resource value (Gherardi 2006), and relied on the quality of the inhabited shell—and not of the offered shell—when presented with a novel one (Tricarico and Gherardi 2007). Field observations (Tricarico and Gherardi 2006) revealed that on arriving at a gastropod predation site, *P. longicarpus* quickly enters an empty shell without prior investigation of it.

In synthesis, our study on one hand confirms that contrary to other hermit crabs species (Elwood 1995; Hazlett 1980, 1987; Neil and Elwood 1986), fighting in *P.*

longicarpus is based on decision rules of the type 'own RV dependency' (Gherardi 2006) and on the other shows for the first time that in this species the experience of a previously held resource plays a relevant role in influencing its agonistic behavior. Taken together, these results underlie the role of resource value as the most important nonstrategic variable in fighting behavior of hermit crabs and other invertebrates (Enquist and Leimar 1987).

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