ORIGINAL ARTICLE

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Fighting behavior in hermit crabs: the combined effect of resource-holding potential and resource value in *Pagurus longicarpus*

Abstract A study was conducted to determine whether asymmetries in both resource-holding potential (RHP) and resource value (RV) influence dominance and fighting behavior in the hermit crab *Pagurus longicarpus*. A total of 120 groups of three crabs were observed for 10 min in four experiments that tested all diverse combinations of equal/different RHP (i.e. 'body size') and equal/different RV (i.e. 'shell size' and 'shell quality'). In a fifth experiment, dominant and subordinate individuals of the same size category (26 groups) were forced to enter shells of opposite quality than those previously occupied, and then the behavior of the reconstituted original groups was observed for additional 10 min. As expected, crabs in lower quality shells were more willing to initiate and to escalate fights. However, their attacks were directed to any crab of the group, independently of the defender's shell quality, and the fight duration did not vary with the different value of the resources at stake. This may indicate that *P. longicarpus* is unable to assess the quality of the shells available in its social environment but bases its tactical decisions during fights solely on its own resource. This suggestion was confirmed by the change in the fighting behavior of crabs whose shell quality was experimentally altered. This manipulation induced an overall increase in the intensity of aggression, drastic modification of crab behavior, and inversion of the hierarchy even though these crabs have had previous experiences of wins/losses and were familiar to the other members of the group. In this species, large crab size and/or the occupancy of adequate (and oversized) shells appeared to be the most likely determinant of contest resolution. Individuals seemed to retain a memory of the previously held resource and behaved accordingly.

Keywords Resource value · Fighting behavior · Dominance · Hermit crabs · *Pagurus longicarpus*

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Introduction

Game theory models predict that fighting between conspecifics is affected in its dynamics by asymmetries that an animal may be able to assess (e.g. Maynard Smith 1974, 1982). Apart from the effects of the different strategies that animals adopt during combats, the relative fighting ability of a contestant [i.e. resource-holding potential (RHP); Parker 1974] has been generally viewed as the main determinant of its winning or losing agonistic encounters. RHP is commonly measured from the animal's relative body size, which most often is a reflection of the relative size of its weaponry (e.g. Caldwell and Dingle 1979; Sneddon et al. 1997). The ability of animals to assess and compare their own RHP with that of their rival, and to make decisions based on the estimated differences, has been the focus of most studies of fighting behavior, and it is integral to some theoretical models of animal conflict—i.e. the asymmetric 'war of attrition' (e.g. Maynard Smith and Parker 1976), and the 'sequential' (e.g. Enquist and Leimar 1983) or 'cumulative assessment' models (Payne 1998).

However, when the outcome of fights cannot be predicted from differences in RHPs or from an animals' ability to assess them, the observed disparity between contestants has been explained on the basis of social dynamics (Chase 1982; Chase et al. 2002) or other asymmetries that may change in the course of fights (Briffa and Elwood 2004), such as the rivals' physiological condition (e.g. Drews 1993; Sneddon et al. 1999; Briffa and Elwood 2002) and their fighting experience ('winner

and loser effects'; Dugatkin 1997). Additionally, empirical evidence from a variety of taxa (reviewed in Taylor and Elwood 2003) suggests that often the dynamics of a contest depends on decision rules based solely on the RHP of the decision maker, rather than on differences in fighting ability between self and the rival (e.g. Taylor et al. 2001). The idea of an individual's 'own RHP-dependent persistence' (Taylor and Elwood 2003) has been incorporated into several theoretical models, e.g. 'war of attrition without assessment' (Mesterton-Gibbons et al. 1996) and 'energetic war of attrition' (e.g. Payne and Pagel 1996) models.

Asymmetries in the quality of the contested resource [resource value (RV)], such as mate, food, nest, or territory, play an additional role in influencing fighting intensity, its duration, and the probability of victory in a wide range of organisms—e.g. shrews (Barnard and Brown 1982), hummingbirds (Ewald 1985), several species of arthropods, amphibians, reptiles, and mammals (citations in Enquist and Leimar 1987), and sand gobies (Lindström and Pampoulie 2005). This may depend on external factors, such as detectable properties of the resource (the 'objective' resource value), and/or on internal factors (the 'subjective' resource value), i.e. the value that the combatant places on that type of resource. Therefore, when a resource yields a high fitness advantage, contest intensity may be relatively high—e.g. in hummingbirds (Dearborn 1998) and honey bees (Gilley 2001), but not in the fallow deer (Jennings et al. 2004)—compared with low-quality resources (e.g. in the speckled wood butterfly; Davies 1978). A previous investment in the held resource may increase its value for the owner (e.g. the nest in the European robin; Tobias 1997), who will be more willing to take risks and to expend time and energy for its defense (e.g. in sand gobies; Lindström and Pampoulie 2005). A disparity between contestants may also derive from the owner being better informed of the value of the resource it possesses than the intruder—e.g. female iguanas competing for nesting burrows (Rand and Rand 1976) or male spiders competing for females (Austad 1983).

Finally, as soon as a dominance hierarchy has been formed, the relatively stable polarity in the outcome of fights may result from a form of recognition between contestants that have had experience at interacting together (Ydenberg et al. 1988). Repeated exposure to an opponent most often reduces fight intensity, e.g. in American lobsters (Karavanich and Atema 1998) and lizards (López and Martín 2001), and usually leads to high-ranking individuals monopolizing a disproportionate share of the available resources (Wittenberger 1981).

Hermit crabs offer an ideal opportunity to study correlates of fighting behavior. The strong association between the majority of hermit crab species (for exceptions see Gherardi 1996a) and empty gastropod shells greatly influences this and almost all aspects of the biology of the species in this taxon (Hazlett 1981). Having a shell of appropriate size and type provides advantages to its inhabitant, the crab being protected from mechanical abuse, dehydration, temperature extremes (Reese 1969; Taylor 1981), salinity changes (Davenport et al. 1980), and predatory pressure (Vance 1972a). A shell that is too small will inhibit growth (Markham 1968; Fotheringham 1976a, b; Bertness 1981a; Angel 2000), reduce protection against predators (Vance 1972a; Angel 2000), and lower survival (Bertness 1981b; Borjesson and Szelistowski 1989) and reproductive success in both males (Hazlett 1989) and females (Childress 1972; Fotheringham 1976b; Bertness 1981a; Wilber 1989; Elwood et al. 1995). On the other hand, a shell that is too large makes locomotion energetically wasteful (e.g. 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 crabs to obtain a shell of appropriate size.

Empty shells (hermit crabs are unable to directly prey on living snails; see, Rutheford 1977, for an exception) are usually in acutely short supply in the habitat (Provenzano 1960; Vance 1972b; Fotheringham 1976c; Kellogg 1976; Scully 1979; for exceptions, see Wilber and Herrnkind 1984; Gherardi et al. 1994). They may be found following snail death at gastropod predation sites (Rittschof 1980a,b; Katz and Rittschof 1993; Rittschof et al. 1995; Gherardi and Atema 2005a), but shells are most often obtained by negotiation (Hazlett 1978, 1980) or interference competition (Hazlett 1966a) with con- and heterospecifics. Several laboratory studies have shown that the decision made by a crab—whether to fight, to escalate an encounter, or to retreat—is based on its ability to assess both shell quality (Elwood and Neil 1992; Hazlett 1996; Wada et al. 1997) and the fighting ability of its opponent (Briffa and Elwood 2000a,b).

Notwithstanding the extensive literature on this topic, there have been few systematic studies (see Elwood et al. 1998; Briffa and Elwood 2001) on the multiple effects of RV, RHP, and other non-strategic variables on hermit crabs' fighting behavior. In the present study, I investigated whether asymmetries in shell quality and body size, together with previous fighting experience and familiarity with the opponents, influenced the agonistic behavior of the hermit crab *Pagurus longicarpus*.

I analyzed the groupings of three crabs arranged into four sets according to the four possible combinations of equal/different body size and equal/different shell quality. It was predicted that crabs occupying low-quality shells should be more willing to take risks fighting crabs in better-quality shells (Hazlett 1970a; Elwood 1995; Gherardi 1996b; Elwood et al. 1998). Larger crabs should be advantaged (Hazlett 1966b, 1970a), but animals having more to gain and therefore being more strongly motivated to escalate fights should be more likely to win. Finally, by experimentally altering the shell quality of crabs that were familiar with each other, it was expected that experience of previous wins/losses and recognition of opponents (Gherardi and Tiedemann 2004a) would play a role in determining the outcome of contests.

Materials and methods

Subjects, collection, and housing conditions

The long-clawed hermit crab, *P. longicarpus* Say 1817, is common in shallow waters along the western Atlantic coasts of North America, from Nova Scotia south to eastern Florida, and in the northern Gulf of Mexico from the west coast of Florida to Texas (Williams 1984).

Between July and August 2003, about 400 hermit crabs with a major chela width (CW) of 0.1–0.4 mm (corresponding to individuals with a shield length of about 4–6 mm) were randomly hand-collected from Little Sippewissett salt marsh (Massachusetts, USA) during diurnal low tides. Immediately after capture, the crabs were separated into small groups and transferred to the Marine Biological Laboratory in Woods Hole, where they were maintained in groups of up to 25 individuals in a temperature-controlled room (22°C) and under a natural 14 L:10 D cycle. They were kept in separate 20-l holding aquaria containing constantly aerated seawater, and fed a diet of commercial shrimp pellets every third day. Water was changed weekly. After being used in the experiments, crabs were released at the collection site.

General methods

Experiments were staged in opaque plastic bowls (10 cm diameter), containing 160 ml unfiltered seawater at 22°C, illuminated during observations by a 75-W incandescent light, 50 cm above the water level. Observations were always conducted between 0900 and 1700 hours.

Two days before the experiments commenced, three intact crabs were selected for each experimental group ('trio'). The animals of each trio were taken from separate holding aquaria to ensure they had no prior knowledge of one another. Sex was not noted, since sex has been shown to exert no effect on agonistic interactions in this and other hermit crab species (Winston and Jacobson 1978; Hazlett 1966b), at least during the non-reproductive period (this species reproduces between October and May with a peak in the autumn; Wilber 1989).

To obtain individuals occupying shells of the proper size for every experiment (see below), crabs were extracted from their original shell by gently breaking it with a bench vise. Each of them was then allowed 4 h alone to choose a new shell from five empty, undamaged, similarly sized shells. These shells were prepared by collecting live periwinkle *Littorina littorea* (the dominant shell type

Table 1 Experimental design

	Animal #1	Animal #2	Animal #3
Expt. 1 (*n*=30)			
Crab size (<>)	L (0.35)	M (0.26)	S (0.15)
Shell size (<>)	L (19.7)	M (17.2)	S (12.6)
Shell quality (=)	OPT	OPT	OPT
Expt. 2 (*n*=30)			
Crab size (=)	M (0.32)	M (0.31)	M (0.31)
Shell size (<>)	L (19.4)	M (17)	S (14.4)
Shell quality (<>)	LTO	OPT	STO
Expt. 3 (*n*=30)			
Crab size (=)	M (0.31)	M (0.31)	M (0.31)
Shell size (=)	M (17.4)	M (17.4)	M (17.4)
Shell quality (=)	OPT	OPT	OPT
Expt. 4 (*n*=30)			
Crab size (<>)	L (0.37)	M (0.3)	S (0.21)
Shell size (=)	M (17.2)	M (17.2)	M (17.4)
Shell quality (<>)	STO	OPT	LTO
Expt. 5 (*n*=26)			
Crab size (=)	M (0.32)	M (0.31)	M (0.31)
Shell size (<>)	S (13.54)	M (16.87)	L (19.46)
Shell quality (<>)	STO	OPT	LTO

The symbols <> and = denote where the crabs of each group differed or were equal in terms of 'crab size', 'shell size', and 'shell quality'. Expt. 5 was a continuation of Expt. 2, using the same individuals. After Expt. 2, animals #1 and #3 were subject to an experimental shell change, leading to the alteration of their quality. So, in Expt. 5 animal #1 occupied STO shells and animal #3 LTO shells

Categories of crab and shell sizes (mean size, in mm, in parentheses): *L* large, *M* medium, *S* small. *OPT* Optimal shells, *LTO* shells that were 10% larger than the optimal shells for a given crab size, *STO* shells that were 10% smaller than the optimal shells for a given crab size, *n* sample size

Fig. 1 Number (**a**) and mean duration (**b**) of fights, average score (**c**), and frequency of strong contacts (**d**) (medians and interquartile ranges) compared among four experiments. Sample size was 30 per experiment. *Letters over bars* indicate the hierarchy obtained by applying multiple comparisons tests to the experiments showing a significant difference after Kruskal–Wallis one-way analyses of variance
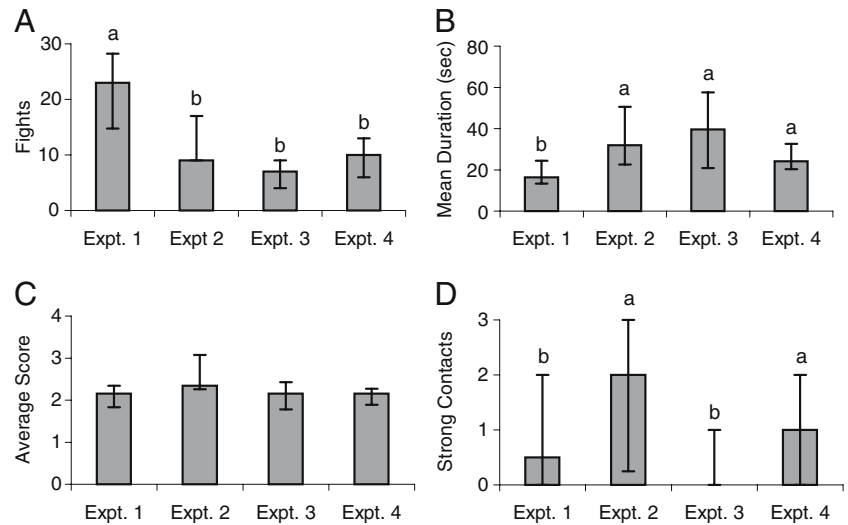
used by the study population), boiling and removing the flesh, rinsing the shells several times in seawater, and air-drying them. Crabs were kept isolated for a total of 2 days, a period that was necessary to reset their social experience. Ten minutes before constituting the trios, the length of antennae and the color of cheliped and pereopod of the three crabs were recorded, and their shells were marked by zero, one, or two dots of permanent black ink to permit identification by the observer.

Experimental design

The influence of 'crab size', 'shell size', and 'shell adequacy' on the fighting behavior of *P. longicarpus* were studied, following in part the design of Gherardi et al. (in press). Crab size (an index of RHP) was estimated from the major chela width (CW, in mm) and was categorized as

large, L (CW>0.33 mm), medium, M (CW=0.23–0.33 mm), or small, S (CW<0.23 mm).

Shells were classified based on size [estimated from their length in mm; shell length (SL)] and their adequacy for the body size of the inhabiting crabs. In fact, although hermit crabs can have preferences for various characteristics of shells (size, species, and amount of damage; see, e.g. Vance 1972a; Bertness 1980, 1981c; Wilber 1990), particularly in the case of the study species (Wilber 1990), size is the most important determinant for shell selection.

Shells were categorized as L (SL>18 mm), M (SL=15–18 mm), and S (SL<15 mm). Shells that were adequate (i.e. optimal, OPT) for crabs of a given size were computed by regressing the equation $y=37.9x+7.3$, where y is SL and x is CW (both in mm). This equation was obtained from a preliminary free-choice experiment in which 192 crabs were separately allowed to choose among five empty shells of different sizes. Shells with a length 10% greater, or 10% smaller, than the OPT for a particular crab were defined

Fig. 2 Frequencies (in percentage) of individuals' (classified per rank) fighting (**a**), attacking a rival (**b**), being attacked by a rival (**c**), and winning (**d**) (medians and interquartile ranges) compared among four experiments. Sample size was 30 per experiment (and per rank). See Fig. 1 for the meaning of *letters over bars*
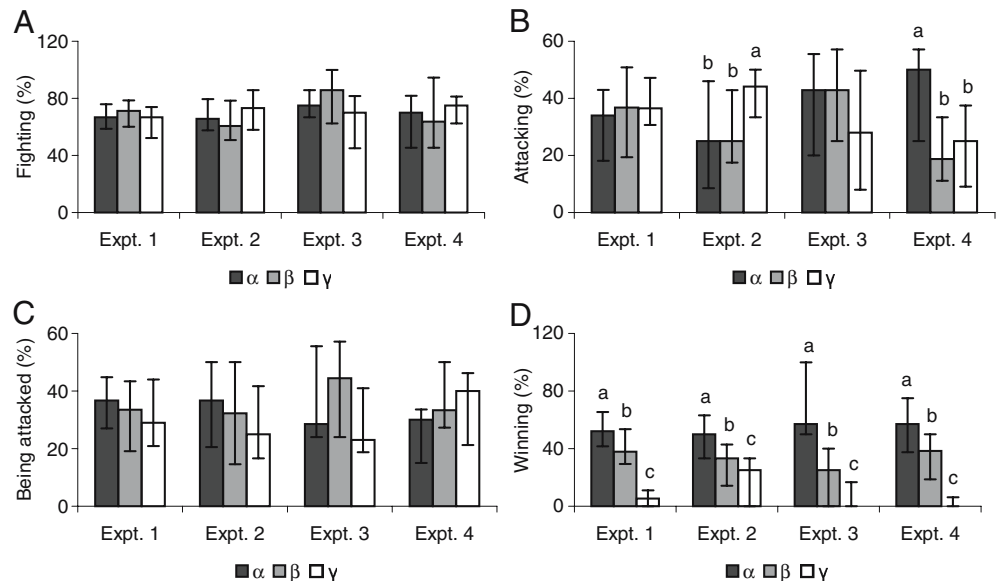
Table 2 Comparisons among ranks (α, β, and γ) in each experiment (Expts. 1–4) for the relative frequencies of individuals' fighting, attacking a rival, being attacked by a rival, and winning

	Expt. 1			Expt. 2			Expt. 3			Expt. 4		
	Fr	P	Hierarchy	Fr	P	Hierarchy	Fr	P	Hierarchy	Fr	P	Hierarchy
Fighting	4.114	0.1278	α=β=γ	4.331	0.1147	α=β=γ	0.738	0.6913	α=β=γ	0.092	0.9549	α=β=γ
Attacking	3.25	0.1969	α=β=γ	**10.294**	**0.0058**	γ>α=β	1.9	0.3867	α=β=γ	**5.645**	**0.0595**	α>β=γ
Being attacked	2.467	0.2913	α=β=γ	3.298	0.1932	α=β=γ	3.524	0.1717	α=β=γ	0.738	0.6913	α=β=γ
Winning	**83.18**	**0**	α>β>γ	**10.683**	**0.0048**	α>β>γ	**24.441**	**0**	α>β>γ	**19.509**	**0.0001**	α>β>γ

Analysis was performed using Friedman two-way ANOVA (Fr statistic, df=2). In the case of significance, a multiple comparisons test was applied to determine the hierarchy. Significant results are shown in bold

as 'larger-than-optimal' (LTO), or 'smaller-than-optimal' (STO) shells. Ranges of crab and shell size used were chosen so that L, M, and S shells were OPT for L, M, and S crabs, respectively.

Four experiments, structured on the basis of crab size, shell size, and shell adequacy, were run on a total of 120 trios (30 per experiment) (Table 1). In Expt. 1, each trio was composed of crabs of three size categories (L, M, and S), each occupying an OPT shell for its size (i.e. L, M, and S crabs inhabiting L, M, and S shells, respectively). Crabs of the trios used in Expt. 2 were of the same M size but differed in terms of the size of their shell (L, M, and S) and hence for their shell adequacy (i.e. LTO, OPT, and STO for crabs in L, M, and S shells, respectively). In Expt. 3, crabs in each trio had the same M size and inhabited the same OPT shell, which was of the M size category. In Expt. 4, trios were composed of L, M, and S crabs inhabiting shells of the same M size and hence of different relative adequacy (i.e. STO, OPT, and LTO shells for L, M, and S crabs, respectively).

Experiment 5 was a continuation of Expt. 2. After 1 day of cohabitation, the shell quality of crabs occupying L and S shells was switched by gently breaking their shells with a bench vise and forcing them to enter a novel shell. This shell was S, and hence STO, for the former crabs in L shells and L, and hence LTO, for the former crabs in S shells. After 4 h apart (not long enough to forget former opponents; Gherardi and Atema 2005a), 26 trios were reconstituted (in the remaining four groups one crab was injured during the manipulation) with the same individuals as in Expt. 2 and observed their behavior for 10 min.

Data collection

Three crabs were placed in the experimental bowl and the events occurring during a 10-min observation period were recorded on a voice tape. Records were later analyzed to obtain the following details:

1. The overall number of fights and the percentage of fights undertaken by each individual. Fights were defined as interactions that started when one crab approached one or two rivals and ended when one or two opponents retreated to a distance greater than 3 cm for at least 10 seconds.
2. The duration of fights (in seconds).
3. The average score. Following in part Gherardi and Tiedemann (2004a), fights were classified as: avoidance (i.e. one opponent retreated with no overt response by the other); threat (i.e. one opponent retreated when the other extended its chelipeds or raised its pereopods or flicked its antennae or chelipeds—when partly withdrawn into the shell); contact (i.e. one opponent retreated after the occurrence of at least one contact behavior, such as antennal contact, grasp, or strike); and shell fight (i.e. one opponent retreated after the other had executed at least one bout of shell rapping

Table 3 Comparisons among ranks (old/new α, β, and old/new γ) in Expts. 2 and 5 for the relative frequencies of individuals' fighting, attacking a rival, being attacked by a rival, and winning (26 trios)

	Expt. 2			Expt. 5		
	Fr	P	Hierarchy old α and γ	Fr	P	Hierarchy new α and γ
Fighting	**6.607**	**0.0368**	γ>α=β	3.322	0.1899	α=β=γ
Attacking	0.905	0.6361	α=β=γ	1.857	0.3951	α=β=γ
Being attacked	1.374	0.5031	α=β=γ	2.574	0.2761	α=β=γ
Winning	**10.336**	**0.0057**	α>β>γ	**30.471**	**0**	α>β>γ

Old α (and old γ) were the individuals that were dominant (and subordinate) in Expt. 2 but became subordinate (and dominant), i.e. new γ (and new α), in Expt. 5 after having been subjected to an experimental shell change (see Table 1). Analysis was done using the Friedman two-way ANOVA (Fr statistic, df=2). In the case of significance, a multiple comparisons test was applied to determine the hierarchy. Significant results are shown in bold
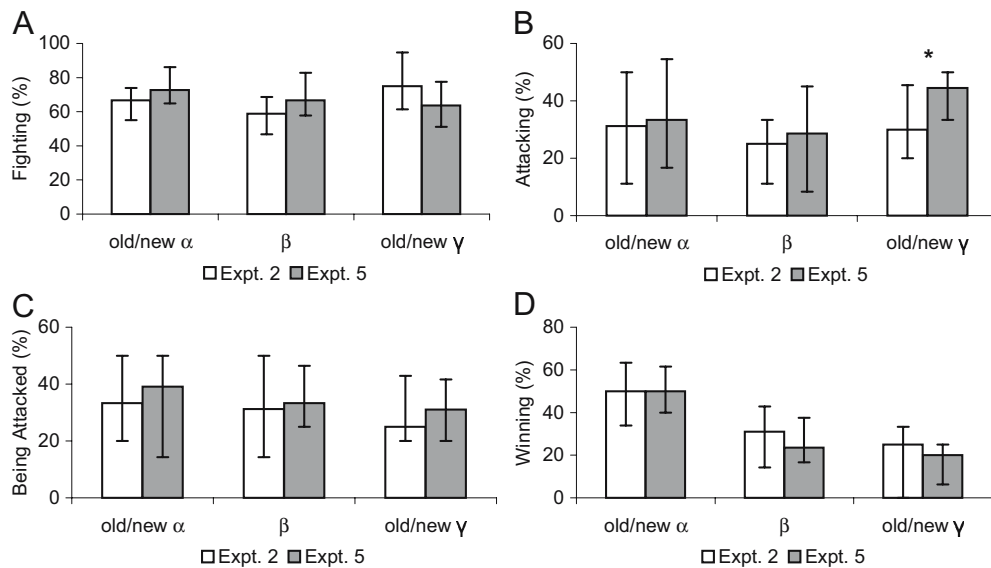
Fig. 3 Frequencies (in percentage) of individuals (classified per rank) fighting (**a**), attacking a rival (**b**), being attacked by a rival (**c**), and winning (**d**) (medians and interquartile ranges), compared between the 10-min observations that preceded (Expt. 2) and followed (Expt. 5) the experimental intervention on α and γ individuals of Expt. 2. This consisted in forcing α individuals of Expt. 2 [old α, originally in larger-than-optimal (LTO) shells] and γ individuals of Expt. 2 [old γ, originally in smaller-than-optimal (STO) shells] to occupy STO and LTO shells, respectively. After the experimental shell change, hierarchy was inverted so that the new α (and the new γ) are the old γ (and the old α) individuals. Sample size was 26 per experiment (and per rank). * means $P<0.05$ after Wilcoxon signed-rank tests

and, eventually, had evicted it from the shell). Each type of fight was ranked on a scale of intensity from 1 to 4. For every 10-min observation, the sum of the scores for each fight was calculated and divided by the number of fights to obtain the average score.

4. The number of grasps and strikes delivered, classified as strong contacts.
5. The occurrence of shell exploration (for a description of shell exploration in *P. longicarpus*, see Scully 1986).
6. Instances of each individual's attacking, and being attacked by, an opponent.
7. The wins recorded by each individual. The winner was the contender that did not retreat at the end of the interaction or that retreated after the other(s) withdrew into the shell.
8. Dominance, measured from the number of wins that each crab gained. From this value, the α (dominant), β, and γ (subordinate) individuals were identified. Dominance reversals were never observed during any 10-min observation.

Data analysis

Nonparametric tests (Sokal and Rohlf 1969; Siegel and Castellan 1988) were applied, because the assumptions of normality and homogeneity of variance were not always met and some measures represented ordinal data. To examine the differences between experiments, Kolmogorov–Smirnov two-sample tests (statistic: KS) and Kruskal–Wallis one-way analyses of variance (statistic: KW) were used. Differences within trios and between Expts. 2 and 5 were analyzed by Wilcoxon signed-rank tests (statistic: z) and Friedman two-way analyses of variance (statistic: Fr) for related samples. When the null hypothesis was rejected after Kruskal–Wallis one-way analyses of variance and Friedman two-way analyses of variance, a multiple comparisons test (Siegel and Castellan 1988) was used to determine which pairs of samples differed significantly. Frequency data were analyzed with *G* tests. Text and figures provide medians and interquartile ranges (first–third quartiles). *P* values of less than 0.05 were considered statistically significant.

Table 4 Comparisons between Expts. 2 and 5 for each rank (old/new α, β, and old/new γ, see Table 3) for the relative frequencies of individuals' fighting, attacking a rival, being attacked by a rival, and winning

	Old/new α		Old/new β		Old/new γ	
	z	P	z	P	z	P
Fighting	−0.876	0.3813	−1.117	0.2638	1.653	0.0983
Attacking	−1.108	0.2678	0.384	0.7008	**1.894**	**0.0582**
Being attacked	0.84	0.4009	−0.706	0.4802	−0.161	0.8722
Winning	−1.461	0.1439	0.401	0.6883	0.865	0.3869

Analysis was done using the Wilcoxon signed-rank test (z statistic). Significant results are shown in bold

Fig. 4 Number (**a**) and mean duration (**b**) of fights, average score (**c**), and frequency of strong contacts (**d**) (medians and interquartile ranges) compared between the 10-min observations that preceded (Expt. 2) and followed the experimental intervention on α and γ individuals (Expt. 5); (see Fig. 3). Sample size was 26 per experiment. ** means $P<0.01$ after Wilcoxon signed-rank tests
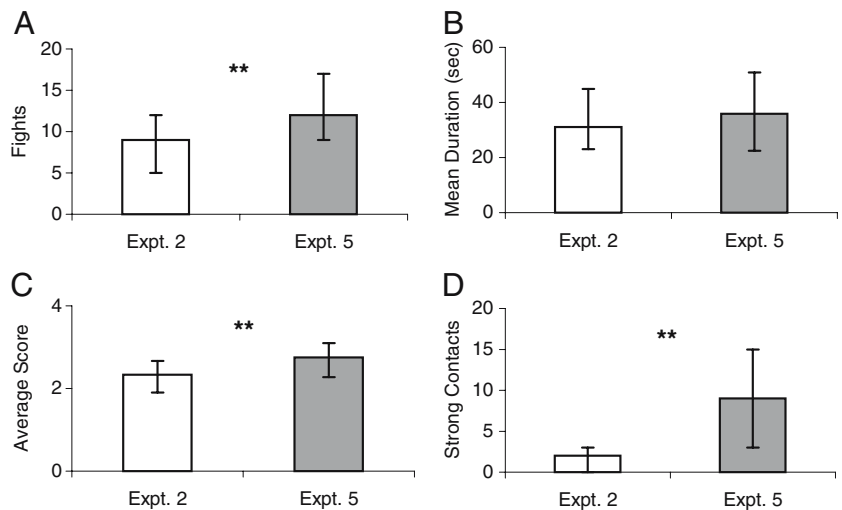
Results

Effect of RV and RHP

Dominant individuals were most often the crabs with L body size that occupied OPT (in Expt. 1, 27 vs. 3) or even STO (in Expt. 4, 30 vs. 0) shells. The influence of crab size on the probability of victory was clear also in Expt. 3. Small differences in shell size (0.1–1 mm) did not seem to influence dominance (α was the crab with a larger shell in 19 of 30 trios, $G=2.124$, $df=1$, $P>0.1$), whereas differences in body size of only 0.01–0.05 mm were sufficient to determine the dominance of the larger crab (21 vs. 9, $G=4.856$, $df=1$, $P<0.05$). In contrast, when the difference in shell size was large (Expt. 2), the individuals occupying larger, but LTO, shells most often won over similarly sized rivals (30 vs. 0).

Fights were significantly more numerous (KW=61.094, $df=3$, $P=0$; multiple comparisons test: Expt. 1>Expt. 2= Expt. 3=Expt. 4) but shorter (KW=31.753, $df=3$, $P=0$; multiple comparisons test: Expt. 2=Expt. 3=Expt. 4>Expt. 1) in Expt. 1 than in all the other experiments (Fig. 1a,b). The four experiments did not differ in the average score for fights (KW=6.158, $df=3$, $P=0.1042$) (Fig. 1c). However, strong contacts were more often executed in Expts. 2 and 4 (KW=12.867, $df=3$, $P=0.0049$; multiple comparisons test: Expt. 2=Expt. 4>Expt. 1=Expt. 3) (Fig. 1d).

Fight duration was expected to be longer when a contestant occupied a low-quality shell, other factors (i.e. hierarchical rank and social environment) being equal. Thus, the fights undertaken by similarly sized α or γ individuals were analyzed and their average duration between instances in which α or γ occupied OPT shells (in Expts. 1 and 3 for α and γ, respectively) and instances in which α or γ occupied STO shells (in Expts. 4 and 2 for α and γ, respectively) were compared. Both α and γ individuals in STO shells fought for a significantly longer time than individuals of the same rank and size in OPT shells (α: KS=0.283, $P=0.0158$; γ: KS=0.267, $P=0.0276$). However, a crab's decision to continue a contest seemed to be relatively independent of the value of the opponent's shell. In fact, in no experiment was there a significant difference in fight duration among the three pairs ($\alpha\beta$, $\beta\gamma$, and $\alpha\gamma$) (Expt. 1: Fr=2.867, $df=2$, $P=0.2385$; Expt. 2: Fr=2.636, $df=2$, $P=0.2673$; Expt. 3: Fr=4.353, $df=2$, $P=0.1134$; Expt. 4: Fr=0.867, $df=2$, $P=0.6483$).

Individuals of different ranks were involved in the same relative number of fights in every experiment (Fig. 2a; Table 2). Only in Expts. 2 and 4, as expected, were attacks most often performed by γ and α, respectively, both occupying STO shells (Fig. 2b; Table 2). However, in none of the experiments were attacks directed at a preferential crab (Fig. 2c; Table 2). Specifically, β and γ individuals did not appear to attack the rival that had a larger or a better quality shell (β in Expt. 1: $z=-1.109$, $P=0.2673$; β in Expt. 2: $z=1.068$, $P=0.2857$; γ in Expt. 2: $z=0.322$, $P=0.7471$).

By definition, α won the majority of fights in all the experiments, followed in the hierarchy by β and γ (Fig. 2d; Table 2). Shell exploration was a rare event, being recorded in 13 instances only (from a total of the 120 trios analyzed).

Effect of win/loss experiences and familiarity with the opponents

In Expt. 2 the individuals occupying LTO and STO shells were α and γ, respectively. After the experimental shell change, the former (old) α (now in STO shells) and the former (old) γ (now in LTO shells) behaved as subordinate (new γ) and dominant (new α) individuals, respectively. In both experiments, crabs of diverse ranks did not appreciably differ for the analyzed parameters, except for the number of fights in Expt. 2 and, obviously, for the number of wins (Table 3). The new α and γ behaved as the old α and γ, as shown from the relative frequencies of the fights (Fig. 3a; Table 4), of the attacks made and suffered (Fig. 3b, c; Table 4), and of the wins gained (Fig. 3d; Table 4). The new γ, which had experienced a higher-quality shell on the previous day, made significantly more attacks than the old γ. However, also in Expt. 5, β's and γ's attacks were

directed to any rival without discrimination (β: $z=1.727$, $P=0.0842$; γ: $z=-1.411$, $P=0.1581$).

The number of fights ($z=-3.246$, $P=0.0012$; Fig. 4a), the average score ($z=-2.707$, $P=0.0068$; Fig. 4c), and the frequency of strong contacts executed ($z=-4.577$, $P=0$; Fig. 4d), but not the mean duration of fights ($z=0.027$, $P=0.9786$; Fig. 4b), were significantly higher after the experimental shell change. This did not seem to be a result of the disturbance inflicted on the crabs through manipulation, because aggression increased in all the individuals, β included (fights: old/new α, $z=-2.926$, $P=0.0034$; β, $z=-3.252$, $P=0.0011$; old/new γ, $z=-2.926$, $P=0.0034$; approaches: old/new α, $z=-2.515$, $P=0.0119$; β, $z=-2.49$, $P=0.0128$; old/new γ, $z=-0.396$, $P=0.692$; strong contacts: old/new α, $z=-3.868$, $P=0.0001$; β, $z=-3.31$, $P=0.0009$; old/new γ, $z=-2.161$, $P=0.0307$).

As in the other experiments, in Expt. 5 shell exploration was a rare event (three out of 26 trios).

Discussion

This study partly corroborates earlier findings showing that, in a large number of animal species, competition for resources is the main trigger for fights between conspecifics (reviewed by Huntingford and Turner 1987). In accordance with Enquist and Leimar (1987), resource value emerged here as an important non-strategic variable in fighting behavior. In fact, shell quality significantly affected the intensity of aggression, as revealed by the frequent strong contacts that crabs executed when occupying shells that were too small (i.e. in Expts. 2 and 4). Also, the individuals inhabiting shells whose size was smaller than optimal ones (γ in Expt. 2 and α in Expt. 4) were highly motivated to initiate fights and to persist with those fights.

These results are not surprising. The suitability of the occupied shells for species, size/volume, and status has been shown to exert a strong effect on intra- and interspecific fighting behavior in the majority of studies conducted so far (Hazlett 1970a,b; Vance 1973; Grant and Ulmer 1974; Hazlett 1978, 1980; Gherardi 1996b). The increased motivation to fight in hermit crabs occupying shells too small by size/volume is also understandable as a behavioral strategy to accommodate individual growth, to protect themselves from predators, and to increase their reproductive success (see references above). However, small crabs, even if highly motivated, did not have a high probability of victory.

In contrast, crabs occupying shells that were too large (in Expts. 2 and 5) only rarely initiated fights and were more likely to be the winners. The potential disadvantages of wearing shells that were too large, e.g. the energetic costs of locomotion (Herreid and Full 1986), may therefore conceal adaptive functions. For instance, by accepting or even selecting an oversized shell crabs may, on one hand, delay the need to find larger shells to assure their growth and reproduction (Childress 1972; Wada et al. 1997; Côté

et al. 1998) and, on the other, gain some fighting advantages. This confirms previous findings in other hermit crab species (Hazlett 1970b), but requires further studies in order to understand if this competitive superiority might be attributable to the shell appearing larger to the opponents or feeling larger to the inhabiting crabs.

When the objective resource value and other factors are equal (see references in Vye et al. 1997; Gherardi and Cioni 2004), body size is important in predicting the outcome of contests even when the larger crab occupies an inadequate shell (Expt. 4) (Hazlett 1966a,b; Elwood and Glass 1981; Dowds and Elwood 1985) and is more important than shell size when differences between contestants are small for these two attributes (Expt. 3). Indeed, a similar large-body size advantage in dominance is widely diffused across the animal kingdom (reviews in, e.g., Caldwell and Dingle 1979; Archer 1988), but proximate causes of this advantage have been largely unexplored.

P. longicarpus inhabiting optimal shells (Expts. 1 and 3) made less frequent use of strong behavioral patterns even if larger shells were available in its social environment (Expt. 1). This proved true, notwithstanding that encounters were relatively more numerous (at least in Expt. 1), probably due to the higher activity of crabs wearing shells of an adequate size for their body. A possible explanation is that in this species motivation to fight changes in response to the subjective—rather than to the objective—resource value. In other words, *P. longicarpus* seems to be more willing to initiate fights and to persist with these fights when it perceives the inadequacy of its own shell rather than when it sees (or it smells, Gherardi and Tiedemann 2004b) other crabs occupying a shell of an absolute higher quality.

Indeed, my results raise doubts about the capacity of this species to finely compare the quality of the domicile shell with the quality of the shells held by the opponents. In fact, I found that hermit crabs were not choosy in their attacks but approached any individual of the group, independently of the defender's resource value. Neither did the crabs seem to gather much information about the contested resource as the fight progresses. In fact, fight duration was independent of the different quality of the shells at stake. Also, shell exploration, consisting here of a quick inspection of the outer surface of shells, was a rare event and rapping (which may be used to assess the defender's shell quality, Hazlett 1980; for other functions, see Elwood and Neil 1992; Briffa and Elwood 2000a,b) was even rarer. These results are in accordance with previous laboratory studies revealing that *P. longicarpus* is inaccurate in distinguishing shells by sight (Gherardi and Tiedemann 2004a), most often switching shells without prior investigation (Scully 1986). A confirmation comes from field observations (Tricarico and Gherardi, personal communication), showing that, upon arriving at a gastropod predation site, *P. longicarpus* quickly enters a novel shell but does not abandon its domicile shell until it has tried the new one. Possibly, 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.

In the overwhelming majority of the species studied so far, fighting crabs were shown, first, to make fine distinctions between a shell available in the habitat and the current domicile shell (e.g. Hazlett 1981; Jackson and Elwood 1989) and, second, to predict their fitness gains from the possession of the opponent's shell. Within the frame of game theory and of other theoretical models (e.g. Parker and Rubenstein 1981; Enquist and Leimar 1983), several authors suggested that the ability to detect and to compare fighting ability and resource value between self and the rival allows hermit crabs to make adaptive decisions, relative to the duration of shell investigation (Neil and Elwood 1986), whether or not to escalate shell fights (Hazlett 1987), and whether to flee or to persist in these fights (Hazlett 1980). A long list of studies confirms the importance of such 'mutual assessment' in the fighting dynamics of several other organisms—e.g. red deer (Clutton-Brock et al. 1979), scorpionflies (Thornhill 1984), and frogs (Burmeister et al. 2002). Conversely, a number of alternative theoretical models describe asymmetric contests in which rivals select persistence based solely on their own RHP (e.g. Mesterton-Gibbons et al. 1996; Payne and Pagel 1996). This idea led to a re-examination of the existing literature and to the identification of several anomalies concerning the mutual assessment theory (Taylor and Elwood 2003). Fighting in *P. longicarpus* might be an additional example of behavior based on decision rules of the type 'own RV-dependent persistency' (in which RV replaces RHP in Taylor and Elwood's 2003 definition).

Experience of dominance and familiarity with similarly sized opponents appear to confer little advantage to individual crabs when the quality of their shells has been experimentally degraded (Expt. 5). This contrasts with results gained from other model organisms (e.g. the crayfish *Procambarus clarkii*), in which recent wins or losses were found to alter the likelihood of an individual winning encounters even when there was a size disparity (Daws et al. 2002). Neither did status recognition (see, e.g. Zulandt et al. 1999; Gherardi and Daniels 2003) nor individual recognition of opponents (Gherardi and Tiedemann 2004a,b; Gherardi and Atema 2005b) have an effect, but winners (and losers) were always the crabs occupying larger (and smaller) shells, notwithstanding their experience of repeated losses (and wins).

However, the memory of shells of different quality may lead to a significant intensification of aggression (more numerous fights, higher average score, more frequent strong contacts and attacks by the new subordinate crab, independent of the defender, in Expt. 5 than in Expt. 2). This was not due to the possible disturbance inflicted on the crabs through their manipulation (it was in fact shown also by β, which was not subject to any manipulation). Crabs (specifically α and γ) seemed to perceive a change from their recent past in the subjective value of the held resource and drastically modified their behavior, the old α, now behaving as γ, and the old γ, now behaving as α. Future studies are needed to rigorously examine whether and how crabs can assess the difference between past and present shells, and behave accordingly.

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