Shell acquisition by hermit crabs. Which tactic is more efficient?

(Article begins on next page)

26 April 2024

ORIGINAL ARTICLE

Elena Tricarico · Francesca Gherardi

Shell acquisition by hermit crabs: which tactic is more efficient?

Abstract Gastropod shells are limited resources for most hermit crab species, acting as primary factors in various aspects of their biology. To investigate the efficacy of different behavioral tactics adopted for their acquisition (locomotion, attendance at shell-supplying sites, interactions with conspecifics in aggregation) we conducted observations and experiments at a salt marsh in New England (USA). Locomotion, fast and meandering, significantly increased the chances of encountering empty shells and conspecifics. However, shell exchanges were rare. Simulated gastropod predation sites quickly attracted a larger number of hermit crabs than the other shell-supplying sites tested (live and dead conspecifics, live snails) and induced the rapid occupancy of all the empty shells offered, usually by the first crabs arriving at the site. Aggregations seemed not to function as shell exchange markets, as previously suggested for several other species. In the short run, exploitation seems to be more efficient for the acquisition of new shells by *Pagurus longicarpus*. In the long run, it is the density of nondestructive gastropod predators that regulates the availability of new shells of good quality in the pool available to this hermit crab species.

Keywords Resources · Locomotion · Shell recruitment · Gastropod predation sites · Hermit crabs · *Pagurus longicarpus*

Introduction

It seems axiomatic that an animal's ability to efficiently acquire resources, such as food, mates, or refuge, is crucial

E. Tricarico · F. Gherardi (✉)
Dipartimento di Biologia Animale e Genetica "Leo Pardi",
Via Romana 17,
50125 Firenze, Italy
e-mail: francesca.gherardi@unifi.it
Tel.: +39-055-2288216
Fax: +39-055-222565

to its survival chances and reproductive potential (Bell 1991). In their efforts to acquire resources, organisms are expected to optimize their use of time, matter, and energy (Pianka 1988). Therefore, natural selection would favor behavioral tactics and strategies that maximize trade-offs between the benefits of possessing resources and the energy expended on searching (and competing over) them, the risks of predation, and the time taken away from other activities.

Gastropod shells are vital for most hermit crab species (exceptions in Gherardi 1996), being essential for their survival, growth, protection, and reproduction (e.g., Fotheringham 1976a; Bertness 1981a; Elwood et al. 1995). The majority of the populations studied to date was shown to chronically suffer from the inadequate supply of inhabitable shells (e.g., Vance 1972a; Fotheringham 1976b; for exceptions see Gherardi et al. 1994) and their growth appears to be largely shell limited (e.g., Bach et al. 1976).

Given their importance for hermit crabs' survival, it is not surprising that shells are acquired and transferred between crabs by several modalities (Hazlett 1996). First, shells, which cannot be acquired by direct predation on living snails (see Rutheford 1977 for an exception), may be found on the substrate (e.g., Vance 1972b; Abrams 1980). However, because of their short supply and low quality (Vance 1972a; Scully 1979; Bertness 1981a; exceptions in Wilber and Herrnkind 1984), this modality does not contribute much to the shell pool available to hermit crabs. Indeed, these shells are soon occupied by other organisms (e.g., octopus or fish; Mather 1982), are often removed from the area by waves and currents, or may be subject to burial by sediments. They can be also damaged by erosion and colonized by epibionts (Wilber and Herrnkind 1984).

Second, shells may be obtained immediately after snail death, in particular after nondestructive snail predation (e.g., Rittschof 1980a,b). This seems to be the unique modality that adds new empty shells to the pool available to hermit crabs. Chemicals released from partly digested snail tissues (Rittschof et al. 1990; Kratt and Rittschof 1991) attract hermit crab species using the prey's shell (Diaz et al.

1995), mostly attracting individuals that are occupying small, badly-fitting, or heavily fouled shells (e.g., Hazlett and Herrnkind 1980; Katz and Rittschof 1993; Gherardi and Atema 2005a). Other attractants are chemical substances contained in the hemolymph of dying con- or heterospecifics (Rittschof et al. 1992; Thacker 1994; Hazlett 1996, 2000) and also the odor of live conspecifics (Gherardi and Atema 2005a).

Third, hermit crabs may acquire new resources, switching shells with other hermit crabs of the same or of a different species (Hazlett 1978, 1980; Bertness 1981b). This modality shuffles shells among the hermit crab population and may have a population-wide homogenizing effect on shell condition and fit over time (McClintock 1985). In several species, shell fighting (e.g., Hazlett 1966a,b; Elwood and Glass 1981) or bargaining (e.g., Hazlett 1978, 1980) often occur at gastropod predation sites. There, the attracted crabs form temporary small aggregations, in which they agonistically interact to establish dominance hierarchies (Winston and Jacobson 1978). The dominant crab obtains the first opportunity to occupy an empty shell as it is released by a predator (McLean 1975); afterwards, the other individuals exchange shells down the hierarchy. Therefore, these aggregations seem to function as "shell markets" and benefit a large number of the gastropod predation site attendants (Rittschof et al. 1992) as the result of a vacancy chain process (Chase et al. 1988).

The present study aims to investigate in the field, for the first time in a systematic fashion, the efficacy of different behavioral tactics adopted by *Pagurus longicarpus* to acquire new shells. Specifically, we analyzed both the dynamics and the success (in terms of shell exchanges) of hermit crabs (1) moving in the habitat, (2) attending shell-supplying sites, and (3) interacting with conspecifics in aggregations. Obviously, these tactics are not mutually exclusive, often being successive stages of the same strategy. In fact, movement may allow crabs to reach shell-supplying sites where they aggregate and interact with conspecifics to acquire new shells.

Materials and methods

The long-clawed hermit crab, *P. longicarpus* Say 1817, is common in shallow waters along the coast of the Eastern United States and in the Gulf of Mexico (Williams 1984). Observations and experiments were conducted in July 2004 in Little Sippewissett salt marsh (Cape Cod, Massachusetts, USA). This is a typical salt marsh of New England, with extensive *Spartina* sp. and *Juncus* sp. zones and a sand–mud substrate. The study area was composed of a pond (surface area of approximately 0.25 ha during low water) connected to the sea by a tidal channel (length: 80 m, width: 9 m). *P. longicarpus* is the only hermit crab species inhabiting the area and mostly occupies periwinkle (*Littorina littorea*) shells.

Movement

Forty-two hermit crabs were haphazardly chosen during diurnal tide cycles and individually tracked by sight for 30 min *in continuum*. We arbitrarily divided tide cycles into four phases, each lasting 3 h, i.e., high tide (HT), ebb tide (ET), low tide, (LT), and flood tide (FT). Observers followed the moving crab at a distance of 1 m in a way that did not disturb it. The observers voice-recorded:

(1) the time spent by each crab in different activities, and specifically in: walking, feeding (i.e., scraping the substrate with chelipeds), and exploring empty shells of *L. littorea*. Less frequent activities (e.g., remaining motionless or interacting with a conspecific) were classified as "others";
(2) the number of conspecifics encountered and the number and type of interactions with them. Following in part Gherardi and Tiedemann (2004a), interactions were categorized 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), weak contact (i.e., one opponent retreated after the occurrence of antennal contacts or touches with chelipeds or pereopods), strong contact (i.e., one opponent retreated after the occurrence of grasps or strikes), and shell fight, characterized by spasmodic shakings (see below) possibly followed by the defender's eviction from the shell;
(3) the occurrence of spasmodic shaking, a behavioral pattern that hermit crabs usually execute during shell fights. In pagurids, it consists of rapid back-and-forth movements of the defender's shell by the attacker's pereopods (Hazlett 1966a);
(4) the number of empty shells encountered;
(5) the number of shell exchanges.

From crab movement, we measured the net displacement from the starting point, ND, the total distance traveled, TD, and the direction of the net displacement along the sea-land axis. TD was computed by multiplying the time spent walking by a crab by the average locomotion speed as assessed in a preliminary experiment. In the laboratory, we had, in fact, measured the time taken by 50 hermit crabs of different sizes to cover a 130-cm long PVC-corridor (10-cm width) containing seawater. This experiment had shown that locomotion speed did not significantly differ with crab size (Kolmogorov–Smirnov two sample test: $ks=0.21$, $p=0.6$) and measured on average 2.2 m/min. We computed the straightness index of the taken path, i.e., the ratio obtained by ND/TD (Batschelet 1981). This ratio would be small if the animal tended to meander and approach 1 if it moved consistently in the same direction.

At the end of the observation period, each tracked crab was collected by hand and preserved in individual vials with 75% ethanol. In the laboratory, the inhabited shell was identified at the species level and its length, SL, was measured to the nearest 0.05 mm using vernier calipers. Although hermit crabs can have preferences for various

characteristics of shells (e.g., size, species), in the case of the study species, size is the most important determinant for shell selection (Wilber 1990).

Crabs were removed from their housing by carefully breaking shells with a vise. Sex was determined and crab size [major chela width (CW)] was measured to the nearest 0.01 mm using a light microscope and an ocular micrometer. Based on their size, crabs were categorized as small (CW≤2.5 mm) or large (CW>2.5 mm) individuals.

For each crab, a shell adequacy index (SAI) was computed. This was obtained from the formula (Gherardi and Vannini 1993):

$$SAI = 100 \times \left(SL_{obs} - SL_{exp}\right)/SL_{exp}$$

where SL_{obs} is the length of the shell actually occupied by an individual, SL_{exp} is the length of the shell which that size of crab "prefers". The size of the preferred shell was given by the equation $y=37.9x+7.3$, where y is SL and x is CW (both in mm), obtained after a preliminary free-choice experiment (Gherardi et al. 2005). The shells used in this and in the other experiments, hereafter, were periwinkles. A SAI close to 100% means that crabs occupy in the field shells near to the preferred size.

Shell-supplying sites

Following in part Rittschof (1980a), we investigated the attraction exerted on crabs by four potential shell-supplying sites. These were simulated using 12 bags (size: 20×20 cm) per treatment made of black mosquito net (mesh size: 2 mm) and filled with stones, and according to the treatment, (1) 10-g snail flesh, generated by freezing for 24 h and thawing (to release proteolytic enzymes; Rittschof 1980b) ten periwinkles, (2) ten live periwinkles, (3) 10-g conspecific flesh generated by crushing on site ten *P. longicarpus* individuals on average, and (4) ten live conspecifics. The results from these experiments were compared with a control, in which 12 bags contained stones only.

Experiments commenced at the beginning of the ET phases (when locomotion is particularly intense), when 12 bags per day were placed 4 m apart at the same level in the intertidal zone of the pond. An empty unfouled, undamaged shell with the appropriate size range (experimental shell) was placed close to each bag. Experimental shells were prepared by collecting live periwinkles, boiling and removing the flesh in the laboratory, rinsing the shells several times in seawater, and air-drying them.

Any crab observed within 30 cm of the shell-supplying site was considered an attendant to the site. Each bag was observed in continuum for 10 min in an hour, two simultaneously. An observer stood motionless next to the site and voice-recorded: latency (the time elapsed from the placing of bags and the first appearance of a crab at a site), the number of site attendants, shell acquisition time (the time elapsed between the first appearance of a crab at a site

and its occupancy of the experimental shell), and the number of shell exchanges. Shell-supplying sites were checked after 1, 2, and 3 h from the beginning of every experiment. The depth of water at a site was about 40 cm at the start and at least 5 cm at the end of each experiment.

Aggregation sites

To stimulate the formation of crab aggregations, we simulated a total of ten periwinkle predation sites, as described above, having an empty intact shell tied with a nylon thread to each bag to avoid its removal from the site. The experimental shell was prepared, as described above, and had the aperture blocked with a resin to impede occupancy by crabs. This precaution was necessary because Rittschof (1980a) reported that hermit crabs were attracted by simulated predation sites but soon left in the absence of an empty shell.

Aggregations were observed for an hour during LT phases. Observers stood motionless next to the site and voice-recorded the number of crabs attending the site every 5 min. We also noted the number and types (as classified above) of interactions between conspecifics, the occurrence of spasmodic shaking, and the frequency of shell exchanges. Focal animals, distinguished by evident shell characteristics, were followed to estimate the time spent in the aggregation site and the number of visits to it.

Density, structure, and shell status of the study population

In the study area, a 50×5 m transect was inspected by two observers during the diurnal LT phase on 31 July, 2004. Crabs in the transect were counted and one specimen for every ten recorded crabs, reaching a total of 100, was collected and preserved in vials containing 75% ethanol. In the laboratory, shell length, crab sex and size, and SAI were determined as described above.

Data analyses

As the assumptions of normality of data and homogeneity of variance were not always met, we used nonparametric tests following the procedures recommended by Siegel and Castellan (1988). For independent samples, Kolmogorov–Smirnov two sample tests (statistic: ks) and Kruskal–Wallis analyses of variance (statistic: H) were used, while related samples were compared using Friedman two-way analyses of variance (statistic: F_r). If differences among samples were significant after the Kruskal–Wallis or Friedman test, we applied Multiple Comparisons tests to determine which pairs of them differed significantly. Nonparametric correlations were made by Spearman rank-order correlation (statistic: r_s). Frequency data were analyzed using G tests after Williams' correction (statistic: G). Text and figures give medians and interquartile ranges (first-third quartiles).

The level of significance at which the null hypothesis was rejected is $\alpha=0.05$.

Results

Movement

Tracked crabs were 16 females and 25 males (the sex of one crab being undetermined) that mostly belonged to the large-size class (34 out of 42) and occupied *L. littorea* shells. In every tide phase except LT ($F_r=19.91$, $df=3$, $p<0.001$), they spent most time walking (HT: $F_r=15.96$, $p=0.001$; ET: $F_r=15.24$, $p=0.002$; FT: $F_r=16.31$; $p<0.001$) (Fig. 1).

Crabs often dug in both mud and sand and remained buried for a certain time before restarting their locomotion (see Rebach 1974). There was no difference between the sexes nor between the size classes (Table 2), but walking appeared more intense during HT and ET than in the other phases (after Multiple Comparisons test: HT=ET>FT>LT). Shell exploration occurred more often at EB (ET> FT=HT>LT), other activities at LT and FT (LT>FT> ET=HT), while feeding was independent of the tide phases (Table 1).

TD was relatively shorter at LT (after Multiple Comparisons test: HT=ET=FT>LT) (Table 1). However, no difference in the extent of TD was found between the sexes nor between the size classes (Table 2). As expected, longer TD corresponded to a higher rate of encounters of both conspecifics ($r_s=0.56$, $t=4.30$, $df=40$, $p<0.001$) (Fig. 2a) and empty shells ($r_s=0.53$, $t=3.95$, $df=40$, $p<0.001$) (Fig. 2b). Overall, 95% (40/42) and 52% (22/42) of the tracked crabs met at least a conspecific and an empty shell, respectively, during their locomotion. However, no crab exchanged its shell with a conspecific and only two occupied the encountered empty shell, both improving their SAI by about 10%.

ND was shorter in LT than in the other phases (after Multiple Comparisons test: HT=ET=FT>LT) (Table 1) and differed between the sexes, but not between the size classes
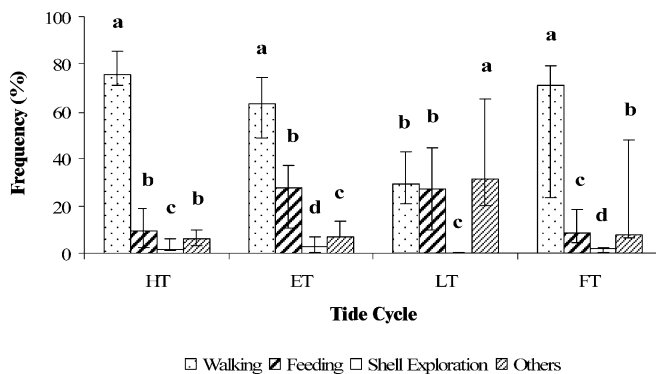

Fig. 1 Relative frequency (medians and interquartile ranges) of the different activities recorded during the four phases of the tide cycle (*HT* high tide, *ET* ebb tide, *LT* low tide, *FT* flood tide). Sample sizes: HT=10, ET=10, LT=11, FT=11. *Letters over bars* denote the hierarchy after Multiple Comparisons tests
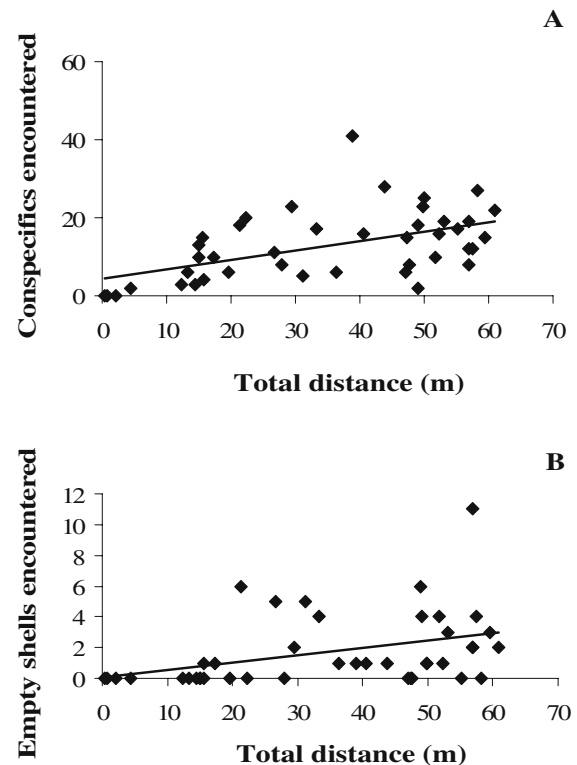

Fig. 2 Relationships between the total distance (*TD*) covered and the number of conspecifics (**a**) and the number of shells (**b**) encountered during locomotion by the 42 tracked hermit crabs

(Table 2). No difference was found in any tide phase between the direction of movement ($G=5.60$, $df=3$, $p>0.1$).

The straightness index did not differ among the tide phases (Table 1) or between the sexes and the size classes (Table 2), and surprisingly, it was not correlated with the number of either conspecifics ($r_s=0.20$, $t=1.30$, $df=40$, $p>0.05$) or empty shells encountered ($r_s=0.10$, $t=0.66$, $df=40$, $p>0.05$). The sexes, but not the size classes, significantly differed for SAI (Table 2). Contrary to our expectations, no correlation was found between SAI and the time spent walking ($r_s=0.23$, $t=1.46$, $df=40$, $p>0.05$), TD ($r_s=0.23$, $t=1.47$, $df=40$, $p>0.05$), ND ($r_s=0.11$, $t=0.70$, $df=40$, $p>0.05$), ND/TD ($r_s=0.08$, $t=0.54$, $df=40$, $p>0.05$), and the number of interactions ($r_s=0.29$, $t=1.93$, $df=40$, $p>0.05$). The only significant relationship found was between SAI and the time spent exploring empty periwinkle shells ($r_s=0.32$, $t=2.15$, $df=40$, $p<0.02$).

The number of interactions between pairs did not differ among the phases of the tide cycle (Table 1) or between the sexes and the size classes (Table 2). Avoidance was the most frequent type of interaction ($F_r=37.54$, $df=3$, $p<0.001$; after Multiple Comparisons test: avoidance>threat> strong contact>weak contact = shell fight) (Fig. 3). We observed only two instances of spasmodic shaking and these were not followed by shell exchange.

Table 1 Comparisons among the four phases of the tide cycle for: the different activities recorded (in %), TD (the total distance covered, in m), ND (the net distance covered, in m), ND/TD (the straightness index), and the number of interactions between conspecifics

		HT	ET	LT	FT	H	df	p
Walking (%)	Median	75.6	63.4	29.4	71.1	11.41	3	**0.01**
	Interquartiles	(70.9–85.5)	(48.7–74.6)	(21.2–43.1)	(23.4–79.1)			
Feeding (%)	Median	9.7	27.9	27.3	8.7	3.82	3	0.3
	Interquartiles	(2.6–18.9)	(10.7–37.3)	(9.9–44.6)	(4.4–18.6)			
Exploring shell (%)	Median	1.7	3	0.1	2.5	8.75	3	**0.03**
	Interquartiles	(1.3–6.1)	(0.4–7.1)	(0–0.5)	(1.9–6.5)			
Others (%)	Median	6.3	7	31.5	8.1	12.06	3	**0.007**
	Interquartiles	(3.3–9.9)	(4.3–10.8)	(20.4–65.2)	(6.5–48.1)			
N° of interactions	Median	11.5	14	10	14	0.03	3	0.99
	Interquartiles	(8.5–17.3)	(5.3–21.5)	(6–21.5)	(7–17.5)			
TD (m)	Median	50.4	42.2	19.6	47.3	11.41	3	**0.01**
	Interquartiles	(47.2–57)	(32.4–49.7)	(14.1–28.7)	(15.6–52.7)			
ND (m)	Median	9.7	9.7	3.7	8.8	8.21	3	**0.04**
	Interquartiles	(3–14.4)	(5.2–20.4)	(1.9–4.3)	(3.7–11.3)			
ND/TD	Median	0.2	0.3	0.2	0.2	3.3	3	0.4
	Interquartiles	(0.1–0.3)	(0.2–0.4)	(0.1–0.3)	(0.1–0.3)			

Analyses used the Kruskal–Wallis test (statistic: *H*). Significant differences are shown in bold. Values are medians (*n* HT/ET=10; *n* LT/FT =11) with interquartile ranges (first-third quartiles)

Attendance at shell-supplying sites

Latency ($H=29.04$, $df=4$, $p<0.001$), the maximum number of attendants at the site ($H=34.56$, $df=4$, $p<0.001$), and shell acquisition time ($H=19.97$, $df=4$, $p<0.001$) differed significantly among treatments, sites with crushed snails being more attractive, followed by sites with both live and dead crabs; less attractive were sites with live snails and the control (after Multiple Comparisons test) (Table 3). In 85% of the analyzed sites (51 out of 60), the experimental shell was acquired by a crab, the lowest rate of acquisition being recorded in the sites with live snails and in the control. Of the 88% of crabs that occupied the experimental shell, none left their former domicile in the site, but, after having

Table 2 Statistical outputs for the comparisons between sexes and size classes (small and large) for the different activities (in %), TD (the total distance covered, in m), ND (the net distance covered, in m), ND/TD (the straightness index), the number of interactions between conspecifics, and shell adequacy index (SAI)

		Sex				Size classes			
		Males	Females	ks	p	Small	Big	ks	p
Walking (%)	Median	44.2	69.7	0.26	0.43	60.1	56.5	0.21	0.89
	Interquartiles	(26.1–71.5)	(22.9–83.5)			(1.1–75.6)	(26.9–78.6)		
Feeding (%)	Median	19.6	11.9	0.18	0.84	12.8	16.4	0.21	0.89
	Interquartiles	(5.1–39.9)	(3.1–27.9)			(6.7–34.6)	(3.8–37.8)		
Exploring shell (%)	Median	0.8	1.9	0.26	0.46	2.7	1.2	0.32	0.42
	Interquartiles	(0.2–2.7)	(0.4–6.4)			(0.8–7.3)	(0.2–2.7)		
Others (%)	Median	8.2	8.9	0.19	0.80	12.3	8.5	0.21	0.87
	Interquartiles	(5.8–37.6)	(5.6–20.6)			(6.9–31.3)	(5.9–30.1)		
N° interactions	Median	11	12	0.19	0.79	11	12.5	0.23	0.82
	Interquartiles	(6–19)	(4.5–17.3)			(4.3–16)	(6.5–18.8)		
TD (m)	Median	29.5	46.4	0.26	0.43	40.1	37.7	0.21	0.89
	Interquartiles	(17.4–47.6)	(15.3–55.6)			(12.7–50.4)	(17.9–51.7)		
ND (m)	Median	3.7	11.3	0.53	**0.005**	11.1	4.7	0.43	0.14
	Interquartiles	(2.4–8.7)	(7.9–19.1)			(7.8–16.8)	(2.9–10.6)		
ND/TD	Median	0.2	0.3	0.24	0.56	0.3	0.2	0.25	0.73
	Interquartiles	(0.1–0.3)	(0.2–0.4)			(0.2–0.3)	(0.2–0.3)		
SAI	Median	−18.2	−12.5	0.84	**<0.0001**	−20	−12.9	0.46	0.1
	Interquartiles	(−20.1, −13.8)	(−19.7, −3.6)			(−25.1, −15.2)	(−23.1, −4.5)		

Analyses used the Kolmogorov–Smirnov test (statistic: *ks*). Significant differences are shown in bold. Values are medians (*n* males=25, *n* females=16; *n* small size=8, *n* large size=34) with interquartile ranges (first-third quartiles)
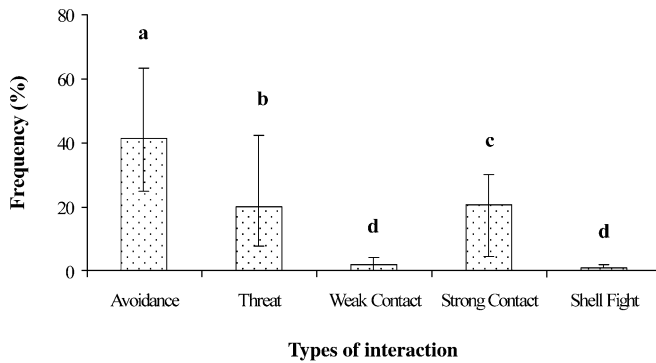
Fig. 3 Frequency (medians and interquartile ranges) of the different types of interaction recorded between pairs of hermit crabs during their movement in the habitat. *Letters over bars* denote the hierarchy after Multiple Comparisons test

Fig. 4 Frequency (medians and interquartile ranges) of the different types of interaction between hermit crabs in aggregations. *Letters over bars* denote the hierarchy after Multiple Comparisons test

entered the experimental shell, seized the old shell with their major chela and immediately took it away from the site. No shell exchange between crabs was ever observed. The number of attendants significantly decreased with time from 9 to 0 ($G=18.86$, $df=7$, $p<0.01$).

Interactions with conspecifics in aggregation

The frequency of crabs attending the site did not significantly change during the hour of observation ($F_r=2.69$, $df=5$, $p=0.75$), neither did the number of interactions decrease with time ($F_r=5.17$, $df=5$, $p=0.40$). We found a significant difference among the types of interactions ($F_r=18.10$, $df=4$, $p=0.001$), with a general low occurrence of strong contacts and shell fights (Fig. 4). Only ten occurrences of spasmodic shaking (out of a total of 969 interactions) were observed. No shell exchange between crabs was ever recorded. The time of attendance at the aggregation site differed greatly among focal individuals ($G=813.64$, $df=10$, $p<0.001$) with 61.3% of the hermit crabs spending less than 2 min and 9.38%, more than 30 min in the site. On average, a crab visited the same aggregation 8.5 times (6–17.5) during an hour ($n=10$).
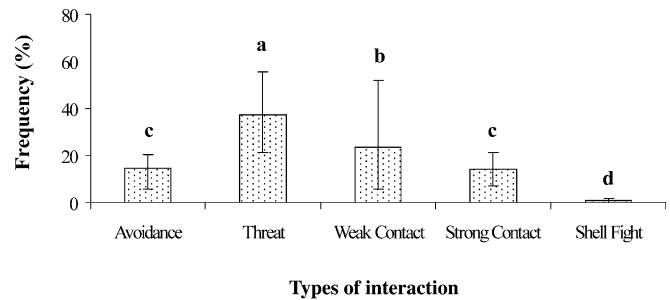
Density, structure, and shell status of the study population

We counted 418 crabs in an area of 250 m^2 (density: 1.7 crab/m^2). The sex ratio significantly favored males (61.7%; 36 females, 58 males, 6 undetermined; $G=5.17$, $df=1$, $p<0.05$). Females, none ovigerous, were smaller than males ($G=23.94$, $df=1$, $p<0.001$), but overall the two size classes were equally represented ($G=0.11$, $df=1$, $p>0.1$; small=41; large=38). SAI did not differ either between the sexes (−16.7% vs −18.9%; ks=0.08, $p=0.5$) or between the size classes (−19.8% vs −14.6%; ks=0.09, $p=0.5$). The average SAI was −18.5% (range: −25.1 and 12.1%, $n=79$). Ninety-seven crabs inhabited *L. littorea* shells, the remaining three occupied shells of *Buccinum* spp. More than 95% of shells were heavily encrusted and damaged. The density of the empty periwinkle shells found in the substrate was 0.02 per m^2 and 71% of them was broken or fouled by algae.

Discussion

The availability of high quality shells is a major force influencing hermit crab population structure and growth (e.g., Vance 1972a,b; Fotheringham 1976c). Our study on the Little Sippewisset population of *P. longicarpus* provides some intriguing results. Crab density was particularly high (1.7 crab/m^2) in the study site, even higher than the density of other populations of the same species (0.9–1.5 crab/m^2; Wilber and Herrnkind 1984)

Table 3 Statistical outputs for the comparisons among the treatments for the arrival of the first attendant at the different shell-recruitment sites (latency), the maximum number of attendants, and the time lapse between the arrival of the first crab and the acquisition of the experimental shell

		Dead crabs	Live crabs	Dead snails	Live snails	Control	H	df	p
Latency (sec)	Median	90	10	0	364.5	135	29.04	4	**<0.001**
	Interquartiles	(0–180)	(0–37.5)	(0–0)	(52–10,801)	(89.5–12,60)			
Maximum n° of attendants	Median	2	2.5	7	1	1	34.56	4	**<0.001**
	Interquartiles	(2–3)	(1.75–3.25)	(5.75–8.25)	(0.75–1)	(0.75–1.25)			
Shell acquisition time (sec)	Median	151	205	48.5	10,801	4,320	19.97	4	**<0.001**
	Interquartiles	(9.75–4,422.8)	(16–3,225)	(27.5–60.5)	(2,474–10,801)	(3,390–5,377.5)			

Analyses used the Kruskal–Wallis test (statistic: H). Significant differences are shown in bold. Values are medians (n of dead crabs=n of live crabs=n of dead snails=n of live snails=n of control=12) with interquartile ranges (first-third quartiles)

inhabiting areas where high quality shells were readily available. This would mean either that the shell status of the Little Sippewisset population is not as poor as assessed (Scully 1979) or, more likely, that it is not subject to strong negative pressures by predation and physical stress. Indeed, hermit crabs in the study site appeared to be shell-limited and subject to severe competition for shells. In fact, the inhabited shells were on average 20% smaller than optimal shells and were often encrusted and damaged. Besides, empty shells on the substrate were scarce with respect to the crab population size and often broken or fouled by algae.

Our study revealed that locomotion rate is particularly high, averaging 2.2 m/min, which is comparable with the speed of 2.5 m/min of radio-tracked *Clibanarius longitarsus* in an East-African mangrove swamp (Gherardi et al. 1990) but decidedly faster than *Clibanarius erythropus* on a Mediterranean shore (0.5–5 cm/min) (Benvenuto et al. 2003). Locomotion of *P. longicarpus* was also time consuming (reaching a maximum of 76%), except at LT, and led individuals to walk for a maximum distance of 60.9 m in half an hour and to displace up to 22.9 m from the starting point. Females covered a longer displacement than males, while crab size had no measurable effect upon any aspect of movement, as found also in *Clibanarius vittatus* (Hazlett 1981b), *Clibanarius tricolor* and *Calcinus tibicen* (Hazlett 1983), *Clibanarius longitarsus* (Gherardi et al. 1990), and *C. erythropus* (Benvenuto et al. 2003). This signifies that even small crabs are capable of rapid long-distance movements and that large/heavy shells do not hamper or make locomotion energetically wasteful (see, on the contrary, Herreid and Full 1986).

P. longicarpus' locomotion was composed of meandering movements (the straightness index averaged 0.2) that differ from the linear, one-way trajectories parallel to the coastline followed by *C. longitarsus* in a mangrove swamp (Gherardi et al. 1990). Movement had no apparent directionality and appeared independent of the tide phase, thus revealing the absence of any migratory component. This contrasts with the behavior of *C. laevimanus*, which regularly moves to the foraging areas when the tide rises, to return to its aggregation sites at ebb tide where it crowds at LW (Gherardi and Vannini 1992).

It seems, therefore, plausible that *P. longicarpus* uses an intense and meandering movement to maximize its probability of intercepting spatially unforeseeable resources. In the time and context of our study, the searched resources were not mates or food. In fact, on the one hand, mating in this species occurs between October and May (Wilber 1989) and no ovigerous females were found in the population. On the other hand, organic detritus in salt marshes does not constitute a limiting resource for an omnivorous detritivore like *P. longicarpus* (Whitman et al. 2001), being abundant and uniformly distributed in the habitat. *P. longicarpus* takes also advantage of detritus in the form of surface foam, feeding upside down in shallow water when surface foam is concentrated (Scully 1978).

Hence, the acquisition of new shells might be the main determinant of hermit crab locomotion. Certainly, the extent of movement (but not the meanderings) increased the chances of crabs encountering empty shells on the substrate but switches to them were rare (two out of 40 encountered empty shells). Besides, the adequacy of the domicile shell (that increased the time spent in exploring the empty shells encountered) was not found to significantly alter crab locomotion, confirming previous laboratory results by Angel (2000) in the same species (on the contrary, in the female *C. vittatus*, shell fit was inversely related to the extent of daily locomotion; Hazlett 1981b).

Shells may be also acquired from conspecific crabs (Hazlett 1978, 1980). Actually, the rate of conspecific encounters was relatively high (at least one conspecific encountered every 30 min) and significantly increased with the extent of movement. But, surprisingly, the interactions among crabs consisted most often of avoidances and threats. Shell fights and, consequently, spasmodic shakings were rare events and no shell exchange was ever recorded.

An additional and possibly higher advantage of the intense and meandering locomotion might be to encounter the chemical stimuli that act in directing crabs to gastropod predation sites or to other shell-supplying sites. At a salt marsh in Florida, Wilber and Herrnkind (1984) clearly proved that most shells are acquired by *P. longicarpus* after gastropod predation on periwinkles. In fact, field experiments demonstrated that the predation on *Littorina irrorata* by ten crown conchs was sufficient to supply the hermit crab population with the same number of shells as the experimental addition in the area of more than 500 empty undamaged shells (Wilber and Herrnkind 1984). The low acquisition rate for substrate-born shells was, in that case, explained by the low probability of a hermit crab chancing across a shell as compared to sensing a predation event when a chemical cue pinpoints the location of a new shell (Rittschof 1980a).

These results are, in great part, confirmed in the present study. Consistent with the several studies by Rittschof and coworkers (e.g., Rittschof 1980a,b; Rittschof et al. 1992), simulated gastropod predation sites were found to quickly attract a relatively larger number of hermit crabs with respect to the other shell-supplying sites and induced the rapid occupancy of all the empty shells offered. Other attractive features were the odors released by live conspecifics, as shown in the same species by Gherardi and Atema (2005a), and by dead individuals, as shown in *C. vittatus* by Rittschof et al. (1992). The latter result apparently contrasts with Gherardi and Atema's (2005a) laboratory finding that *P. longicarpus*, inhabiting either high or low quality shells, reacts to the odor of freshly dead conspecifics with the typical antipredator behavior of remaining inactive (Rittschof and Hazlett 1997). This might suggest that attraction and repulsion are signaled by the same substance whose meaning changes with time or, alternatively, by different substances emitted in sequence. Finally, *P. longicarpus* did not react to the odor of live snails as compared to that of the control; indeed, only one species (Rutheford 1977) has been recorded removing living snails from their shell.

On first arriving at a shell-supplying site, crabs were observed to switch to the novel shell without prior investigation. They soon left the site, usually taking the former domicile shell away to abandon it on the substrate at a certain distance. In part, this is not surprising (Scully 1986) because crabs attracted to gastropod predation sites often inhabit shells that are smaller or in poorer condition than the majority of individuals in the population and are, therefore, highly motivated to quickly switch shells (Rittschof et al. 1995). In laboratory experiments, *P. longicarpus* was shown to be inaccurate in distinguishing shells by sight (Gherardi and Tiedemann 2004a) and individuals in badly-fitted shells did not appear to be choosy in their attacks towards conspecifics but approached any individual of the group, independently of the defender's resource value (Gherardi 2006). Neither did crabs seem to gather much information about the contested resource as the fight progresses (Gherardi 2006) and possibly an appreciation of its quality may be gained only by wearing the new shell. The question remains as to why crabs remove the old domicile shell from the site.

Whatever the answer is, this behavior has important ecological implications for the hermit crab population. In fact, the odor released by dead gastropods or dead/live conspecifics can attract other crabs to the site for at least 3 h. But due to the absence of any vacated shell, no chain processes are possible as predicted by the theory (Chase et al. 1988) and observed in the laboratory (Hazlett 1979) and field (McLean 1975): the old domicile shell, once abandoned on the substrate far away, can be subject to those factors that remove empty shells from the crab population (erosive damage, burial by sediment, colonization by harmful epibionts, and occupancy by other organisms) if not used in due time.

Aggregations, per se, seemed not to function as shell exchange markets for *P. longicarpus* as has been suggested for several other species (e.g., *C. laevimanus*, Gherardi and Vannini 1993; *C. erythropus*, Gherardi and Benvenuto 2001). In our field experiments, we observed between-crab interactions of low agonistic intensity and no shell exchanges. Notwithstanding, the time of crab attendance at the aggregations was relatively long and crabs often visited the site several times. Previous laboratory experiments have also shown that *P. longicarpus* is capable of chemically recognizing an opponent (Gherardi and Tiedemann 2004a,b; Gherardi and Atema 2005b) and can associate the odor of a conspecific with the quality of its shell (Gherardi et al. 2005). This form of individual recognition has an adaptive meaning, exclusively within a social context. An explanation of this apparent paradox might be that, although shell swapping is a rare event, once it occurred, the benefit for an individual is so high as to justify the seemingly antieconomical behavior of attending aggregation sites and of having evolved refined systems of social recognition.

Conclusions

The present study shows that attendance of hermit crabs at shell-supplying sites is a behavioral tactic increasing *P. longicarpus*' likelihood of access to new shells. Crabs may also crowd in aggregations to swap shells, an event that, although rare, could be highly beneficial to the usurper if made with the right conspecific (i.e., the conspecific inhabiting a high quality shell that the usurper is able to recognize in the crowd). The individuals taking advantage of shell-supplying sites are usually the first crabs arriving at the site and/or occupying the vacant shell. Therefore, in the short run, locomotion seems to be more efficient for the acquisition of new shells by *P. longicarpus* than either aggression or mutualism through negotiation (Hazlett 1981a). From a behavioral point of view, the efficacy of exploitative, rather than direct, competition might explain why locomotion in this species is so intense in all size classes. From an ecological perspective, our results suggest that, in the long run, it is the density of nondestructive gastropod predators that regulates, through a top–down process, the entry of new shells of good quality in the pool available to *P. longicarpus* and, therefore, influences the structure and growth of its populations.

References

Abrams P (1980) Resource partitioning and interspecific competition in a tropical hermit crab community. Oecologia 46:365–379

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

Bach CE, Hazlett BA, Rittschof D (1976) Effects of interspecific competition on fitness of the hermit crab *Clibanarius tricolor*. Ecology 57:579–586

Batschelet E (1981) Circular statistics in biology. Academic, New York

Bell WJ (1991) Searching behaviour. Chapman and Hall, London

Benvenuto C, Sartoni G, Gherardi F (2003) Foraging behaviour of the hermit crab *Clibanarius erythropus* in a Mediterranean shore. J Mar Biol Assoc UK 83:457–461

Bertness MD (1981a) Predation, physical stress and the organization of a tropical rocky intertidal hermit crab community. Ecology 62:411–425

Bertness MD (1981b) Competitive dynamics of a tropical hermit crab assemblage. Ecology 62:751–761

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

Diaz H, Orihuela B, Rittschof D, Forward RB Jr (1995) Visual orientation to gastropod shells by chemically stimulated hermit crabs, *Clibanarius vittatus* (Bosc). J Crustac Biol 15:70–78

Elwood RW, Glass CW (1981) Negotiation or aggression during shell fights of the hermit crab, *Pagurus bernhardus*. Anim Behav 29:1239–1244

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

Fotheringham N (1976a) Population consequences of shell utilization by hermit crabs. Ecology 57:570–578

Fotheringham N (1976b) Hermit crab shells as a limiting resource. Crustaceana 31:194–197

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

Gherardi F (1996) Non-conventional hermit crabs: pros and cons of sessile, tube-dwelling life in *Discorsopagurus schmitti* (Stevens). J Exp Mar Biol Ecol 202:119–136

Gherardi F (2006) Fighting behavior in hermit crabs: the combined effect of resource-holding potential and resource value in *Pagurus longicarpus*. Behav Ecol Sociobiol 59:500–510

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

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

Gherardi F, Benvenuto C (2001) Clustering behaviour in a Mediterranean population of the hermit crab *Clibanarius erythropus*. Ophelia 55:1–10

Gherardi F, Tiedemann J (2004a) Binary individual recognition in hermit crabs. Behav Ecol Sociobiol 55:524–530

Gherardi F, Tiedemann J (2004b) Chemical cues and binary individual recognition in the hermit crab, *Pagurus longicarpus*. J Zool Lond 263:23–29

Gherardi F, Vannini M (1992) Hermit crabs in a mangrove swamp: clustering dynamics in *Clibanarius laevimanus*. Mar Behav Physiol 21:85–104

Gherardi F, Vannini M (1993) Hermit crabs in a mangrove swamp: proximate and ultimate factors in the clustering of *Clibanarius laevimanus*. J Exp Mar Biol Ecol 168:167–187

Gherardi F, Micheli F, Vannini M (1990) Movement patterns and dispersal of the hermit crab *Clibanarius longitarsus* in a mangrove swamp. Mar Behav Physiol 16:209–223

Gherardi F, Zatteri F, Vannini M (1994) Hermit crabs in a mangrove swamp: the structure of *Clibanarius laevimanus* clustering. Mar Biol 121:41–52

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

Hazlett BA (1966a) Social behavior of the Paguridae and Diogenidae of Curacao. Stud Fauna Curacao Other Caribb Isl 23:1–143

Hazlett BA (1966b) Factors affecting the aggressive behavior of the hermit crab *Calcinus tibicen*. Z Tierpsychol 23:655–671

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

Hazlett BA (1979) Individual distance in Crustacea: IV. Distance and dominance hierarchies in *Pagurus pollicaris*. Mar Behav Physiol 6:225–242

Hazlett BA (1980) Communication and mutual resource exchange in North Florida hermit crabs. Behav Ecol Sociobiol 6:177–184

Hazlett BA (1981a) The behavioral ecology of hermit crabs. Ann Rev Ecolog Syst 12:1–22

Hazlett BA (1981b) Daily movements of the hermit crab *Clibanarius vittatus*. Bull Mar Sci 31:177–183

Hazlett BA (1983) Daily movement in the hermit crabs *Clibanarius tricolor* and *Calcinus tibicen*. J Crustac Biol 3:223–234

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

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

Hazlett BA, Herrnkind W (1980) Orientation to shell events by the hermit crab *Clibanarius vittatus* (Bosc) (Decapoda, Paguridea). Crustaceana 89:311–314

Herreid CF, Full RJ (1986) Energetics of hermit crabs during locomotion: the cost of carrying a shell. J Exp Biol 120:297–308

Katz J, Rittschof D (1993) Alarm/investigation responses of hermit crabs as related to shell fit and crab size. Mar Behav Physiol 22:171–182

Kratt CM, Rittschof D (1991) Peptide attraction of hermit crabs *Clibanarius vittatus* Bosc: roles of enzymes and substrates. J Chem Ecol 17:2347–2365

Mather J (1982) Choice and competition: their effects on occupancy of shell homes by *Octopus joubini*. Mar Behav Physiol 8:285–293

McClintock TS (1985) Effects of shell condition and size upon the shell choice behavior of a hermit crab. J Exp Mar Biol Ecol 88:271–285

McLean R (1975) A description of a marine benthic faunal habitat web: a behavioral study (Ph.D. dissertation). Florida State University, Florida

Pianka ER (1988) Evolutionary ecology. Harper and Row, New York

Rebach S (1974) Burying behavior in relation to substrate and temperature in the hermit crab, *Pagurus longicarpus*. Ecology 55:195–198

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

Rittschof D (1980b) Enzymatic production of small molecules attracting hermit crabs to simulated predation sites. J Chem Ecol 6:665–676

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

Rittschof D, Kratt CM, Clare AS (1990) Gastropod predation sites: the role of predator and prey in chemical attraction of the hermit crab *Clibanarius vittatus*. J Mar Biol Assoc UK 70:583–596

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

Rittschof D, Sarrica J, Rubenstein D (1995) Shell dynamics and microhabitat selection by striped legged hermit crab, *Clibanarius vittatus* (Bosc). J Exp Mar Biol Ecol 192:157–172

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

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

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

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

Siegel S, Castellan NJ Jr (1988) Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York

Thacker RW (1994) Volatile shell-investigation cues of land hermit crabs: effect of shell fit, detection of cues from other hermit crab species, and cue isolation. J Chem Ecol 20:1457–1482

Vance RR (1972a) Competition and mechanism of coexistence in three sympatric species of intertidal hermit crabs. Ecology 53:1062–1074

Vance RR (1972b) The role of shell adequacy in behavioral interactions involving hermit crabs. Ecology 53:1075–1083

Whitman KL, McDermott JJ, Oehrlein MS (2001) Laboratory studies on suspension feeding in the hermit crab *Pagurus longicarpus* (Decapoda: Anomura: Paguridae). J Crustac Biol 21:582–592

Wilber TP Jr (1989) Associations between gastropod shell characteristics and egg production in the hermit crab *Pagurus longicarpus*. Oecologia 81:6–15

Wilber TP (1990) Influence of size, species and damage on shell selection by the hermit crab *Pagurus longicarpus*. Mar Biol 104:31–39

Wilber TP, Herrnkind WF (1984) Predaceous gastropods regulate new-shell supply to salt marsh hermit crabs. Mar Biol 79:145–150

Williams AB (1984) Shrimps, lobsters, and crabs of the Atlantic coast of the Eastern US, Maine to Florida. Smithsonian Institution, Washington DC

Winston M, Jacobson S (1978) Dominance and effects of strange conspecifics on aggressive interactions in the hermit crab *Pagurus longicarpus*. Anim Behav 26:184–191