

Foraging behaviour of the hermit crab *Clibanarius erythropus* in a Mediterranean shore

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Field studies were carried out along a Mediterranean rocky shore to describe the foraging behaviour of the hermit crab *Clibanarius erythropus*, a common intertidal Diogenidae. The spatial strategy adopted during foraging activity was investigated through monitoring the movement of ten individuals, each followed for two hours. This revealed that hermit crabs maximized the space explored while in search of food and that shell type was one factor influencing the extent of movement. The evaluation of hermit abundance on different algal substrates provided clues to understanding the pattern of food utilization. This study shows that 'generalist' hermit crabs display a certain degree of selectivity, mostly foraging on assemblages of filamentous algae and corticated macrophytes. The conclusion is that *C. erythropus* selects substrates where good foraging can occur; whether hermit crabs eat within the selected substrates every food item they encounter or select food at the level of individual items is still an unanswered question.

INTRODUCTION

Most ecological and behavioural studies on hermit crabs have focused on both crab–shell interactions and shell assessment (e.g. Elwood & Neil, 1992). So far, relatively little work has been done on the foraging habits of these decapods. Most hermit crabs are defined as generalist in their diet and opportunistic in their feeding habits. They are viewed as detritus sediment feeders (Orton, 1927; Roberts, 1968; Greenwood, 1972; Caine, 1975, 1976), but are also classified as macrophagous, scavengers, predators (Kunze & Anderson, 1979; Hazlett, 1981a), and/or meso-grazers (Ruesink, 2000). They feed on organic debris, decayed and fresh macro-algae with associated fauna and epiphytic algal flora, small invertebrates, and macroscopic pieces of dead and live animal tissues.

Motility obviously enhances the efficiency in foraging, food often constituting the principal determinant of movement, as shown in *Clibanarius vittatus* (Hazlett, 1981b). Among sedentary hermit crabs, different adaptations are developed, such as filter feeding on suspended matter (Markham, 1977; Schuhmaker, 1977; Caine, 1980; Gherardi, 1994, 1996). A further opportunistic behaviour was shown in the benthic detritivore *Pagurus longicarpus*, where a detrital foam floating on the water surface has been described (Scully, 1978).

The present work furnishes data on the feeding habit of *Clibanarius erythropus*, a common intertidal Diogenidae living in the Mediterranean, Black Sea and along the Atlantic coast from Brittany to the Azores (Zariquiey Alvarez, 1968). We followed the patterns of movement displayed by a sample of *C. erythropus* while in search of food, and identified the algal assemblages where foraging mostly occurred.

MATERIALS AND METHODS

The study was carried out in the Baia Domiziana rocky shore (Monte Argentario, Italy, 46°26'50"N and

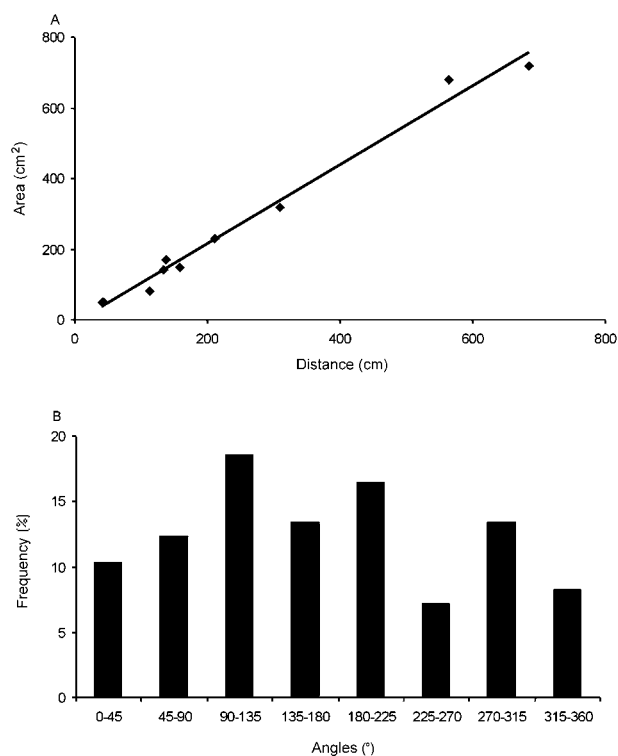
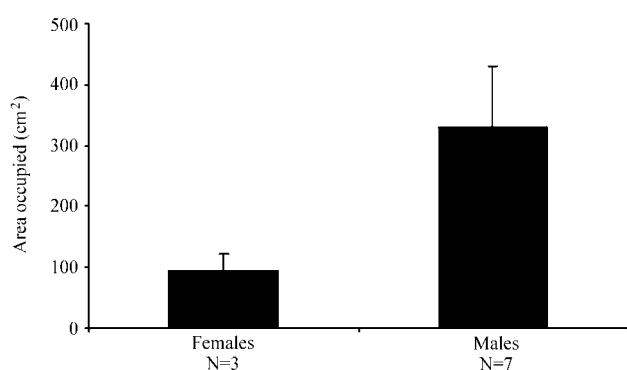


Figure 1. Patterns of movement of foraging *Clibanarius erythropus*: (A) correlation between the covered distance and the occupied area; and (B) frequency distribution of the angles followed every 10 min.

Table 1. *Movement of ten Clibanarius erythropus followed for two hours: details on each hermit crab followed.*

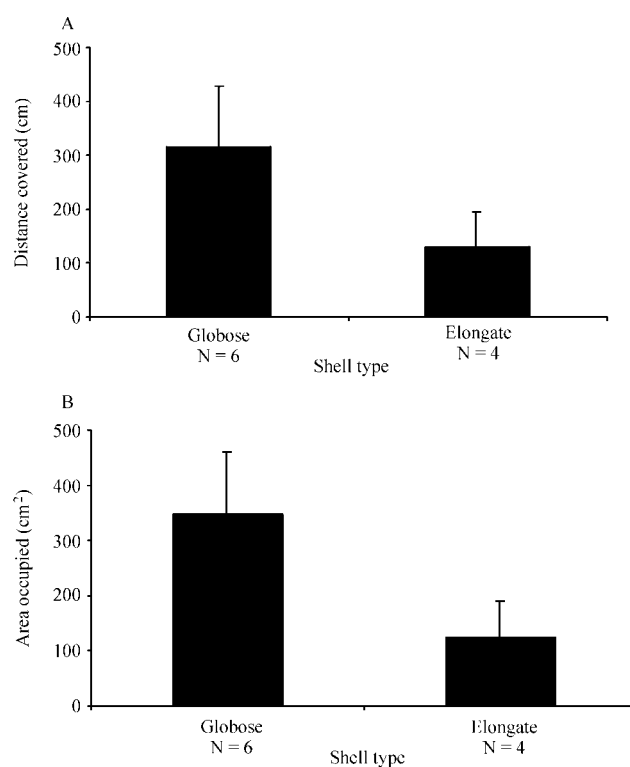
Hermit	Sex	Shield (mm)	Area (cm ²)	Total distance (cm)	Degree of linearity
1	male	3.09	140	134.0	0.42
2	female	2.18	50	42.5	0.72
3	male	2.76	320	310.0	0.20
4	female	1.33	80	113.0	0.48
5	male	2.75	680	564.0	0.60
6	male	4.13	230	212.0	0.75
7	male	1.54	50	42.0	0.58
8	male	2.48	170	137.5	0.47
9	female	1.75	150	158.5	0.26
10	male	2.06	720	685.0	0.05

Hermit	Shell	Weight (g)	Length (mm)	Width (mm)	Type
1	<i>Gibbula</i> sp.	0.34	10.0	11.1	globose
2	<i>Cerithium</i> sp.	0.26	14.2	6.3	elongate
3	<i>Cerithium</i> sp.	1.42	25.0	12.5	elongate
4	<i>Pisania</i> sp.	0.45	15.7	8.0	elongate
5	<i>Gibbula</i> sp.	0.28	10.4	9.6	globose
6	<i>Monodonta</i> sp.	1.44	15.7	14.3	globose
7	<i>Pisania</i> sp.	0.32	14.4	7.3	elongate
8	<i>Gibbula</i> sp.	0.23	8.1	9.6	globose
9	<i>Gibbula</i> sp.	0.18	7.7	7.2	globose
10	<i>Gibbula</i> sp.	0.22	8.7	8.1	globose

**Figure 2.** Patterns of movement of foraging *Clibanarius erythropus*: comparison between sexes in the occupied areas (average \pm SE).

11°09'E) (for details on the study site see Benvenuto & Gherardi, 2001).

During July 1996, the movements of ten hermit crabs during their foraging activity were analysed during different days and hours (ranging 1000–1600), three to five metres away from the coast line. Each animal was followed for two hours. At the beginning of the observation and every ten minutes thereafter, a nail with a floating numbered buoy was carefully inserted onto the substrate adjacent to the observed hermit crab, obviously avoiding any disturbance to it. In this way, it was possible to redraw the followed path by each specimen at the end of each session of observation, thus measuring distances and angles, the total distance covered, and the area occupied. The area was measured by representing the path on a reference grid and then summing the 100 cm² quadrats occupied by each hermit. The degree of linearity of the path (computed as the ratio between the total distance

**Figure 3.** Patterns of movement of foraging *Clibanarius erythropus*: comparison between types of shells in (A) the covered distances (average \pm SE), and (B) the occupied areas.

covered and the distance between the starting and the final locations) was also measured.

At the end of each session of observation, hermits were collected, preserved in 75% alcohol, and then examined in the laboratory to determine sex and size (shield length),

Table 2. Classes, orders, species, and functional groups of the algae sampled in the study area.

Class	Order	Species	Functional group
Chlorophyceae	Caulerpales	<i>Halimeda tuna</i> (Ellis & Solander)	6
	Cladophorales	<i>Chaetomorfa aerea</i> (Dillwyn)	2
		<i>Cladophora</i> sp.	2
		<i>Cladophora prolifera</i> (Roth)	2
	Siphonocladales	<i>Valonia utricularis</i> (Roth)	2
Fucophyceae	Dictyotales	<i>Dictyota</i> sp.	3.5
		<i>Dictyota dichotoma</i> (Hudson)	3.5
		<i>Padina pavonica</i> (L.)	3.5
	Fucales	<i>Sargassum vulgare</i> C. Agardh	5
	Sphacelariales	<i>Cladostephus spongiosus</i> (Hudson)	4
		<i>Halopteris filicina</i> (Grateloup)	4
		<i>Sphacelaria cirrosa</i> (Roth)	2
		<i>Stypocaulon scoparium</i> (L.)	4
Rhodophyceae	Ceramiales	<i>Alsidium corallinum</i> C. Agardh	4
		<i>Alsidium helminthocorton</i> (Schwendimann)	4
		<i>Halopithys incurva</i> (Hudson)	4
		<i>Herposiphonia secunda</i> (C. Agardh)	2
		<i>Polysiphonia</i> sp.	2
	Corallinales	<i>Amphiroa rigida</i> J.V. Lamouroux	6
		<i>Corallina elongata</i> Ellis & Solander	6
		<i>Halitilon virgatum</i> (Zanardini)	6
		<i>Jania adhaerens</i> J.V. Lamouroux	6
		<i>Jania rubens</i> (L.)	6
		<i>Peyssonnelia</i> sp.	3.5
	Cryptonemiales	<i>Peyssonnelia squamaria</i> (S.G. Gmelin)	3.5
	Gelidiales	<i>Gelidium pusillum</i> (Stackhouse)	4
	Gigartinales	<i>Caulacanthus ustulatus</i> (Turner)	4
		<i>Feldmannophycus rayssiae</i> (Felmann & Feldmann-Mazoyer)	4
		<i>Hypnea musciformis</i> (Wulfen)	4
	Rhodymeniales	<i>Champia parvula</i> (C. Agardh)	4
		<i>Rhodymenia ardissoni</i> Feldmann	4

to identify the inhabited shells at the genus level (following D'Angelo & Gargiullo, 1978), and obtain measurements (weight, length, and width). On the basis of their length:width ratio (Benvenuto & Gherardi, 2001), shells were classified as globose (if the ratio was <2) or elongate.

To determine the time when foraging activity was more intense, during July 1995 the number of hermits was recorded using four 70×70 cm grids (overall surface 19,600 cm²) haphazardly located at 4, 5, 6 and 22 m away from the coast line, during three time periods (1100–1400, 1400–1700 and 1700–2000) on four consecutive days. At the peak time, in three of the above grids and during three consecutive days, observations were conducted to analyse the foraged substrata: the number of hermit crabs was recorded in each 100 cm² quadrat of the grid and samples of the algal community were collected for each quadrat, fixed in 10% seawater formalin, and then determined in the laboratory. Algae were classified on the basis of anatomical and morphological characteristics (functional groups). Following Steneck & Dethier (1994), we distinguished the following functional groups: 1, (microalgae); 2, (filamentous algae); 3, (foliose algae); 3.5, (corticated foliose algae); 4, (corticated macrophytes); 5, (leathery macrophytes); 6, (articulated calcareous algae); and 7, (crustose algae). (Numbers, as reported by Steneck

& Dethier (1994), indicate morphology: a higher number corresponds to an increased anatomical complexity.) Analysis was limited to multicellular algae.

RESULTS

Patterns of movement

The analysis of the general patterns of movement displayed by hermit crabs in their foraging bouts of activity showed that the distance covered and the area occupied were positively correlated (Pearson correlation test: $r=0.993$, $df=8$, $P<0.01$), and that the frequency distribution of angles was uniform (Wilks test: $G=8.149$, $df=7$, $P>0.1$) (Figure 1A,B).

Table 1 summarizes the data collected for each hermit crab followed. The Mann–Whitney U -test was used to compare sexes and types of the inhabited shells. No male–female difference was recorded in the total distance covered (females: average=104.67±33.74 cm, $N=3$; males: average=297.79±90.80 cm, $N=7$; $U=5$, n.s.), neither did the sexes differ in the degree of linearity of their path (females: average=0.484±0.132, $N=3$; males: average=0.437±0.091, $N=7$; $U=9$, n.s.). Females occupied wider areas than the males (females vs males:

Table 3. Algal functional groups organized in six super-groups (letters) and the number of *Clibanarius erythropus* found foraging on them.

Functional group	A	B	C	D	E	F
2	X	X	X		X	X
3.5	X	X		X	X	
4	X	X	X		X	X
5		X				
6	X	X	X			
Area (cm ²)	8700	2100	1900	300	500	2200
Hermit crabs/cm ²						
Mean	0.70	0.17	0.16	0	0	3.00
Standard error (SE)	0.18	0.09	0.09	0	0	1.38

93.33 ± 29.63 m² vs 330 ± 100.57 m²; $U=3.5$, $N=3,7$, $P\sim 0.05$) (Figure 2).

Hermits inhabiting globose shells covered longer distances than those found in elongate ones (315.17 ± 99.71 cm vs 129.12 ± 65.45 cm; $U=4$, $N=6, 4$, $P\sim 0.05$), and occupied wider areas (348.33 ± 112.05 m² vs 125 ± 65.38 m²; $U=4$, $N=6, 4$, $P\sim 0.05$) (Figure 3A,B), but did not differ in the degree of linearity of the followed path (0.423 ± 0.101 vs 0.493 ± 0.109; $U=10$, $N=6, 4$, n.s.).

Hermit size and shell weight did not influence the distance covered (Spearman rank correlation test: $r_s=0.406$, $t=1.257$, n.s.; $r_s=-0.103$, $t=0.293$, n.s.), the area occupied ($r_s=0.427$, $t=1.337$, n.s.; $r_s=-0.064$, $t=0.18$, n.s.), or the degree of linearity ($r_s=0.164$, $t=0.164$, n.s.; $r_s=0.358$, $t=1.083$, n.s.).

Substrates occupied while foraging

Table 2 lists all the species of algae collected, classified on the basis of the functional groups we distinguished here. No foliose algae were found. We defined as super-groups those assemblages of functional groups occurring together in our samples.

Table 3 shows the six super-groups we classified, their coverage in the 15,700 cm² sampled area, and the number of hermit crabs per cm² found foraging on them between 1400 and 1700. This was the period when foraging activity reached a peak (0.94 foraging hermit crabs per 100 cm² vs 0.39 and 0.55 at, respectively, 1100–1400 and 1700–2000; one-way analysis of variance (ANOVA): $F=4.314$, $df=2$ & 634 , $P<0.05$), and also corresponded to the time of the minimum water level (averaged during the study period: 0.088 m vs 0.189 m and 0.252 m at, respectively, 1100–1400 and 1700–2000). The Kruskal–Wallis (KW) one-way ANOVA revealed that the substrate covered by the super-group F (composed by filamentous algae and corticated macrophytes) was significantly more crowded with hermit crabs (KW=11.959, $df=5$, $P<0.05$).

DISCUSSION

This work represents the first attempt to analyse the foraging behaviour of one species of hermit crabs through field observations conducted on undisturbed individuals.

Our assumption was that the patterns of movement that animals display while searching for food allow the characterization of the foraging strategy adopted. The analysis of movement was here integrated with the classification of the substrates where foraging occurred.

During *Clibanarius erythropus*' foraging activity, the explored area increased with the distance covered, the angular change in direction was uniform, and the path followed displayed a low degree of linearity. All these patterns are expected for foragers that aim at increasing their probability of finding food items when these are patchily distributed (Gherardi et al., 2001). These patterns of movement did not depend on hermit crabs' sex and size, similarly to that described in *Clibanarius vittatus* (Hazlett, 1981b), *C. tricolor* and *Calcinus tibicen* (Hazlett, 1983), and *Clibanarius longitarsus* (Gherardi et al., 1990).

As far as the characteristics of the inhabited shells were concerned, on one hand their weight had no influence on the extent of locomotion (contrary to the semi-terrestrial species *Coenobita compressus*; Osorno et al., 1998; Herreid & Full, 1986). On the other, the occupation of globose shells made hermit movement faster, possibly because of the greater reduction of friction. A previous study (Gherardi & Benvenuto, 2001) showed that globose shells were also preferred by hermit crabs of the same species, if either globose or elongate empty shells were introduced into a cluster.

One result emerging from the analysis of the patterns of movement is that *Clibanarius erythropus* does not appear to forage randomly in the habitat and does not consume food as encountered; that is, its behavioural mechanism does not follow the foraging models of 'no selection' or of 'passive acceptance' (Pyke et al., 1977).

A prevalence of foraging hermit crabs was found on those algal assemblages where the functional groups 2 (filamentous algae) and 4 (corticated algae) occurred. A number of hints suggest that these groups may constitute favourite substrates (as well as potential food items) for the hermit crab foragers. The group 4 is composed of turf-forming species developing a protected habitat for other species; epiphytic organisms—including some filamentous algae of the group 2—growing on group 4 algae and the fine particles trapped on them can be food sources for hermit crabs. In their structure and chemistry (being soft

and without toxins), as well as in their morphology (having a relatively simple thallus form) (Littler & Littler, 1980), the algae belonging to the group 2 appear digestible, palatable, and easy to handle for hermit crabs. We also found that assemblages were more crowded of hermits where these two algal groups were exclusively present, possibly because there the density of the favoured food items is higher and, as a consequence, the time of 'patch departure' seems longer (Pyke et al., 1977).

Thus, the conclusion is that *C. erythropus* selects substrates where foraging can occur; whether hermit crabs eat within the selected substrates every food item they encounter or select food at the level of individual items is still an unanswered question.

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