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Effects of chemical context on shell investigation behavior in hermit crabs

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Abstract

Specific chemicals in the environment evoke significant changes in the behavior of many aquatic organisms. We studied in the laboratory whether satiated individuals of the hermit crab, *Pagurus longicarpus* Say 1817, adjust their investigatory behavior towards an empty, optimal gastropod shell according to differences of chemical context. We also explored to what extent shell investigation by a crab in the same hunger state was affected by occupying an inadequately sized shell. Our results confirmed in part previous findings that crabs can discriminate the odor of freshly dead snails from the odor of freshly dead conspecifics. In the presence of the former odor, crabs inhabiting shells of inadequate size were more responsive and active than those in better-fitting shells. To the contrary, regardless of the quality of the inhabited shell, *P. longicarpus* remained practically motionless when presented with the odor of freshly dead conspecifics, possibly because the risks of incurring in predators would outweigh the benefits of acquiring a new shell. Unexpectedly, we found that crabs in both types of shell quality exhibited nearly the same behavior in control water, while crabs in adequate shells were more responsive in the presence of food odor. Individuals appeared insensitive to the odor of live snails; indeed, only one hermit crab species has been seen removing living snails from their shells. An intriguing result was that water conditioned by the odors of live conspecifics exerted a strong effect on all the individuals by inducing an intense shell investigation. Our study underlines the central role exerted by chemical detection in hermit crabs' behavior and demonstrates the existence of a complex interplay among chemical context, the physiological state of the animal, and the ecological pressures of the habitat.

Keywords: Behavior; Chemical context; Chemical sensing; Hermit crabs; *Pagurus longicarpus*; Shell fit

1. Introduction

Specific chemicals in the environment evoke significant changes in the behavior of aquatic organisms of many different taxa and functional groups (reviewed in Mackie and Grant, 1974; Daloze et al.,

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1980; Atema, 1985). Facets of hermit crabs' behavior that are known to be affected by external chemicals mostly include those associated with searching for and acquiring new and better-fitting shells, both activities that dominate the biology of this taxon (reviewed in, e.g., Hazlett, 1981; McLean, 1983).

An abundant body of literature shows that aquatic hermit crabs are attracted to gastropod predation sites by the means of chemical substances (McLean, 1974; Rittschof, 1980a,b; Lepore and Gilchrist, 1988; Rittschof et al., 1992) and that their orientation towards shells is mediated by a combination of chemical and visual cues (Hazlett and Herrnkind, 1980; Hazlett, 1982; Diaz et al., 1994; Orihuela et al., 1992; Chiussi et al., 2001). Starting from the observations of McLean (1975) and Rittschof (1980a), evidence has been accumulating that their attraction to the sites that are potential sources of shells is affected by predator odors (Rittschof and Hazlett, 1997) and is specific for certain preferred gastropod species (Diaz et al., 1995). Also, site attraction depends on the quality and fit of the shell the animal inhabits (Hazlett and Herrnkind, 1980; Gilchrist and Abele, 1984; Rittschof et al., 1992; Katz and Rittschof, 1993); in other words, the responses by crabs to chemical substances in the medium may be the expression of their motivation to obtain new shells (Elwood, 1995; Elwood et al., 1998). Recently, Gherardi and Tiedemann (2004) showed that hermit crabs can even recognize familiar and unfamiliar conspecifics by the use of individual odors. This result is indicative that our knowledge of the chemical ecology of this taxon is still provisional and warrants further research.

The present study aims at investigating, for the first time in a systematic fashion, the influence that chemical substances in the environment exert on the behavioral responses of hermit crabs to one of their most important resources: empty shells. To this end, we described the response that satiated individuals show towards an empty optimal shell in the presence of five different odors (live and freshly dead conspecific odor, live and freshly dead snail odor, the odor of the usual food) and of raw seawater as a control. Test crabs occupied well-fitting shells–selected by the animals themselves from a wide size range of otherwise intact shells–or shells of an inadequately small size. We predicted that, in the same hunger state, individuals inhabiting adequate shells would always be scarcely motivated by a new shell potential, while those in inadequate shells would approach and investigate the offered shell regardless of odor ambience.

2. Methods

In August 2003, 40 adult *Pagurus longicarpus* Say 1817 with a shield length of 5–6 mm were hand-collected haphazardly from Little Sippewissett salt marsh (Cape Cod, Massachusetts, USA) during diurnal low tides. Once in the Marine Biological Laboratory at Woods Hole (Massachusetts, USA), crabs were housed in a temperature controlled room (22 °C) under a natural 14L:10D cycle and maintained individually for no more than 2 weeks until used in opaque plastic bowls (10 cm in diameter) containing 160 cc unfiltered, standing seawater; water was changed daily. Crabs were fed a diet of dried shrimp pellets twice a week. Sex was not noted; however, sex-ratio was approximately 50% at the collection site and no mating behavior was observed during the study. In fact, reproduction in this species occurs between October and May with a peak in autumn (Wilber, 1989). After being used in experiments, crabs were released back into the collection site.

Crabs were randomly assigned to one of two groups that differed for shell fit, i.e. crabs occupying shells of either (1) adequate (AS) or (2) inadequate size (IS). These two groups were obtained by forcing individuals (whose original shells were gently broken with a vise) to occupy new unfouled and undamaged shells, half of which were classified as adequate, the other half as inadequate. The shell size (the shell base-apex axis, y) that we considered adequate to the crab size (the width of its major chela, x) was computed from the equation: $y=37.9x+7.3$. The parameters of this equation were obtained from a free-choice experiment, in which a total of 192 hermit crabs (major chela width: 0.1–0.4 mm) were given a choice of 5 shells of different size (size range: 10–25 mm) per individual (following Angel, 2000). On the other hand, those periwinkle shells with a base-apex axis of about 2/3 the length of a corresponding adequate shell were classified as inadequate.

The offered shell was prepared by collecting live periwinkle *Littorina littorea* (the dominant shell type

used by the study population), boiling and removing the flesh, rinsing the shells in seawater, and air-drying them. The experiment ended after 48 h of free access to shells, when crabs ceased exploring and moving into new shells.

Every hermit crab, belonging to either the AS or the IS group, was subject to 6 successive odor treatments, the sequence of which was systematically varied between crabs during 6 consecutive days: live (LH) and freshly dead (DH) conspecific hermit crabs, live (LS) and freshly dead (DS) snails, food odor (FO), and, as a control, raw seawater (WA). Solutions of odors from live organisms were obtained immediately prior to use by keeping 5 live *P. longicarpus* crabs (LH) or 5 live *L. littorea* snails (LS) for 12 h in 100 cc seawater. Stock solutions of hermit crab flesh (DH) were generated by crushing, macerating for 1 h at room temperature, and then filtering with coarse filter paper 3 g (ca. 2 g dry weight) of crabs per 100 cc seawater. To generate stock solutions of snail flesh (DS), we incubated (and then filtered following Rittschof, 1980b) frozen and then thawed pieces of *L. littorea* flesh in seawater for 1 h at room temperature in the ratio of 3 g (ca. 2 g dry weight) flesh/100 cc seawater. Food solution (FO) was made by macerating 2 g of dried shrimp pellets (the same used to feed the test crabs) in 100 cc seawater and filtering with coarse filter paper.

Tests were conducted in opaque plastic bowls (10 cm in diameter) containing either 1 cc of one of the five test solutions diluted in 100 cc of standing seawater or 100 cc of raw standing seawater. The experimental bowl was provided with an empty periwinkle shell of adequate size placed with its apex upwards. The shell was prepared as described above for the free-choice experiment; it was boiled and rinsed in seawater several times to eliminate any possible odor and its aperture was blocked with a resin to avoid its occupation by the crab. Preliminary observations had shown that resin and its odor had no effect on shell attractiveness. Tests started with the insertion of an individual into the bowl at about 8 cm from the shell.

The events occurring during 5 min of observation were described on a tape recorder and later analyzed to obtain: (1) latency (the time taken for the crab to first enter in contact with the shell; when a crab never investigated the shell, we arbitrarily assigned a time equal to 305 sec); (2) time motionless; and (3) duration of shell investigation.

During observations, which were performed between 0900 and 1600 h, bowls were illuminated by a 75-W overhead incandescent light, 50 cm over the water level. Between tests, every crab was maintained in its individual bowl and fed with 0.5 g of dried shrimp pellets to keep them satiated.

Statistical analyses were performed following the procedures found in Sokal and Rohlf (1969) and in

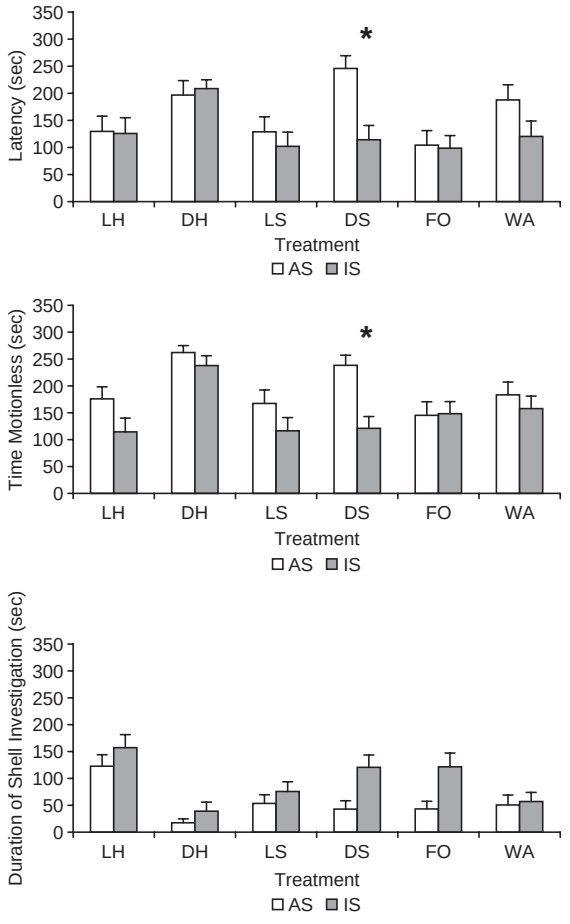

Fig. 1. Mean (+1 S.E.) latency, time motionless, and duration of shell investigation compared among treatments and between satiated *Pagurus longicarpus* occupying two categories of shell, i.e. adequate (AS) or inadequate shells (IS). The analyses were done on the responses of test crabs towards an empty, optimal shell of the periwinkle *Littorina littorea*. For treatments, we mean the solutions contained in the experimental bowl that were produced from live (LH) and freshly dead (DH) conspecifics, live (LS) and freshly dead (DS) snails, and shrimp pellets as food (FO). Raw seawater (WA) was the control. * denotes a significant difference after Student's *t*-test on $\ln(x+1)$ transformed data between AS and IS of at least $p<0.008$ (Bonferroni correction).

Underwood (1997). All data were checked for normality and homogeneity of variance using Cochran's *C*-test and were ln(x+1) transformed to remove heteroscedasticity. The effects of treatments and shell quality were examined by a two-way repeated measures ANOVA. Where significant *F*-ratios were calculated by ANOVA, Student–Newman–Keuls' multiple comparisons test (SNK) was applied to identify which data sets were different. The comparison between the two categories of shell quality per treatment was made on ln(x+1) transformed data by Student's *t*-test (statistic: *t*), the probability of error being adjusted by Bonferroni correction. *P* values of less than 0.05 (less than 0.008 after Bonferroni correction) were considered significant.

3. Results

Overall, crabs in AS had a longer latency, and spent more time motionless and less time investigating the offered shell than crabs in IS; we also found main treatment effects for these three measures and, in the case of latency, a significant interaction in the patterns of difference among treatments versus the two categories of shell quality (Fig. 1, Table 1). Latency was significantly longer for crabs inhabiting IS in the presence of DH than with the other solutions and with WA, while DS (together with DH) made AS crabs less ready to react to the offered shell if compared with the behavior shown in the majority of the other treatments, particularly in FO. DH had a stronger effect than the other treatments also for the other measures recorded, causing for both crab groups longer time motionless and shorter duration of shell investigation. An opposed pattern was found with LH; in this context, we recorded shorter time motionless than in presence of DH and longer duration of shell investigation than in all the other treatments. Latency (t=3.209, df=38, p<0.0027) and time motionless with DS (t=3.313, df=38, p<0.0020) were significantly longer in AS than in IS, while the other comparisons between AS and IS were never significant (t between 0.144 and 2.489, p 0.8859–0.0173).

4. Discussion

This laboratory study confirms previous findings (Rittschof, 1980a,b; Rittschof et al., 1992) that *P.*

Table 1
(a) Results from a two-way repeated measures ANOVA testing for differences in mean latency, time motionless, and duration of shell investigation when hermit crabs were presented with six treatments (factor T) and inhabited either adequate (AS) or inadequate (IS) shells (factor Q)

	Latency				Time motionless				Duration of shell investigation			
	df	MS	*F*-ratio	*p*	*df*	MS	*F*-ratio	*p*	*df*	MS	*F*-ratio	*p*
(a)												
Shell quality=Q	1	11.230	**7.5002**	**0.0000**	1	10.539	**4.7582**	**0.0004**	1	30.1857	**8.1729**	**0.0000**
Treatment=T	5	8.325	**5.5604**	**0.0193**	5	15.281	**6.8997**	**0.0093**	5	33.9453	**9.1908**	**0.0027**
QxT	5	4.728	**3.1574**	**0.0090**	5	4.785	2.1605	0.0597	5	4.9897	1.3510	0.2443
Residual	209	1.497			209	2.215			209	3.6934		
Total	220				220				220			
Standard error for means	0.2736				0.2353				0.3039			
(b)												
SNK	AS:	DH=DS>LH=LS=WA>FO			AS and IS:	DH>DS=FO=LH=LS=WA			AS and IS:	LH>DS=FO=LS=WA>DH		
	IS:	DH>DS=FO=LH=LS=WA										

For treatments, we mean five solutions containing odor of: live conspecifics (LH), freshly dead conspecifics (DH), live snails (LS), freshly dead snails (DS), and food (FO); the sixth treatment was raw seawater (WA) as the control. Prior to the analyses, data have been transformed to log(x+1). (b) Hierarchies of treatments after Student–Newman–Keuls' multiple comparisons tests (SNK). For latency where the interaction Q×T was significant, the analyses were done by comparing the means of the factor T separately at each level of the factor Q (AS, IS). For time motionless and duration of investigation where the interactions Q×T were not significant, the analyses were done on the means of the factor T averaged over the two levels of the factor Q (AS and IS). Significant values in bold.

longicarpus can discriminate chemical substances of different source and meaning, an ability that it shares with the few other hermit crab species whose chemical ecology has been studied so far (*Clibanarius vittatus*: Rittschof, 1980a,b; Hazlett, 1982; Rittschof et al., 1992; Katz and Rittschof, 1993; Rittschof and Hazlett, 1997; *Diogenes avarus*: Hazlett, 1997; *Pagurus annulipes*: McLean, 1974, 1975; *Pagurus novazealandiae* and *P. traversi*: Hazlett, 2000; *Pagurus pollicaris*: McLean, 1974, 1975; Rittschof et al., 1992). More interestingly, our results provide a new insight on the complex interplay existing among chemical context, the physiological state of the animal, and the ecological pressures of the habitat.

First, we demonstrated that *P. longicarpus* is able to detect odors given off from freshly dead gastropods or from freshly dead conspecifics. This result is not surprising, since several previous studies (Rittschof, 1980b; Rittschof, 1990; Rittschof et al., 1990; Kratt and Rittschof, 1991; Rittschof, 1993) have shown that hermit crabs respond to chemical substances (that do not comprise feeding cues; Carr, 1967), either generated by the digestive action of predators on prey gastropod flesh (Rittschof, 1980b; Rittschof et al., 1990) or contained in the hemolymph released by injured con- or heterospecific individuals (Rittschof et al., 1992; Small and Thacker, 1994; Thacker, 1994; Hazlett, 1996; Hazlett, 2000). The ability to detect these chemicals has a clear adaptive value. On the one hand, crabs can chemically identify the sites where shells are likely available; in these sites, shells can also be obtained by aggression or mutual exchange (Hazlett, 1970a,b, 1983) with other individuals (also heterospecifics, Hazlett et al., 1996) that have been similarly attracted. And many crabs would benefit from the cascade of shell exchanges resulting from a vacancy chain process (Chase et al., 1988). On the other hand, animals can associate these odors with dangers from potential predators (and stronger conspecifics) and behave accordingly by avoiding the sites of odor provenience.

The different response to these chemical cues might depend on the physiological state of the crabs and, specifically, on the quality of their shell. So, we expected that the occupation of shells of poor quality would in any case induce in them a behavior aimed at maximizing the probability of obtaining new shells; in these animals, odors from dying shell-bearer organisms would stimulate positive responses towards the offered shell. To the contrary, for crabs occupying shells of good quality, the same cues would act as alarm substances and their behavior would be directed to minimize the risks of incurring in predators and in other, eventually dominant, individuals. These predictions have been met in previous studies, in which the quality of the inhabited shell was found to modulate crab behavior. For instance, at the interspecific level, the faster appearance at predation sites of *C. vittatus* than *P. longicarpus* was related to the former species occupying less adequate shells than the latter (Rittschof, 1980a). At the intraspecific level, the crabs attracted by predation sites and by alarm odors were those individuals with small (Rittschof et al., 1992; Katz and Rittschof, 1993; Gilchrist and Abele, 1984; Hazlett, 2000), badly fitting (Rittschof, 1980a; Katz and Rittschof, 1993), or heavily fouled shells (Hazlett and Herrnkind, 1980).

Confirming in part the above predictions, we found that crabs inhabiting shells of inadequate size were more responsive and active (cf. Angel, 2000) than those in better-fitting shells in the presence of odors generated by snail flesh. The importance for *P. longicarpus*' biology to rely upon this mechanism of shell recruitment has been proved in a field study conducted in a salt marsh in Florida by Wilber and Herrnkind (1984): the surprisingly high rate of new, well-fit shell acquisition (occurring in 4–5% of the hermit crabs sampled each night) was imputed to the combined effect of predation by *Melongena corona* on *Littorina irrorata* and attraction by *P. longicarpus* to predation sites. However, these mechanisms of shell recruitment seem to have scarce effects on the hermit crab population under study here that, to the contrary, appeared subject to a severe competition for shells (nearly 30% of crabs were found in shells of inadequate size, F. Gherardi, pers. obs.).

Against our expectations and contrary to Rittschof et al.'s (1992) results from a population of the same species, we found that *P. longicarpus* inhabiting shells of either good or bad quality remained practically motionless when presented with the odor released by dead conspecifics. Immobility is a typical anti-predator behavior in hermit crabs (Rittschof and Hazlett, 1997): by not moving, crabs

significantly reduce the chance of being detected by predators that prey by sight. An explanation of our results could be that, at least for satiated individuals (to the contrary, hungry crabs treated in a similar way show clear feeding responses; J. Atema, pers. obs.), odors emitted by dying or freshly dead conspecifics signal a danger and act as alarm substances in areas where predatory pressures are strong. In other words, in the population under study here, the risks of being seen by one of the many species preying on *P. longicarpus* (Weissberger, 1995) might outweigh the benefits of acquiring a new shell. Therefore, the meaning assigned to the same chemical substances seems to vary across populations possibly as a consequence of the different ecological pressures acting in the diverse habitats.

Unexpectedly, individuals inhabiting shells of both qualities exhibited nearly the same behavior in control water, while the occupancy of adequate shells made individuals more responsive in the presence of food odor. Finally, crabs seemed to be insensitive to the odor of live snails; indeed, only one species (Rutherford, 1977) has been seen removing living snails from their shells. In contrast, we found that the odor emitted by live conspecifics stimulated longer shell investigations in both crab groups. This datum suggests that hermit crabs can recognize live conspecifics by odors (Gherardi and Tiedemann, 2004) and that this ability possibly increases the likelihood of shell exchanges between individual crabs.

In essence, our study underlines the central role played by chemical detection of hermit crabs in maintaining the gastropod shell habitat web (McLean, 1975; 1983). Similarly to other invertebrate aquatic taxa (Stenzler and Atema, 1977), chemical information interacts in a complex way with both the physiological state of a hermit crab and the ecological pressures of its habitat to induce specific and adaptive responses (Brönmark and Hansson, 2000).

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