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Land hermit crabs use odors of dead conspecifics to locate shells

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Abstract

A series of experiments at two tropical locations tested the ability of land hermit crabs *Coenobita perlatus* (H. Milne Edwards) and *Coenobita compressus* (H. Milne Edwards) to detect and respond to odors of dead conspecifics. An attraction array compared numbers of crabs attending hidden food odors and dead conspecific odors. Pit experiments tested crab shell-acquisition behaviors at different hidden odors. Bucket experiments confined crabs collected from various categories (feeding crabs, wandering crabs and crabs aggregated at dead conspecific odors) and tested behavioral responses to odors and an empty shell. Land hermit crab behavior at both sites was similar. Crabs were attracted to dead conspecific odors up to 10 times more than to food odors. Crabs attracted to dead conspecifics displayed significantly more shell-acquisition behaviors: touching other crab's shells in an exploratory manner and switching shells if an empty shell was available. In buckets, crabs from each category switched into shells. Results are compared to previous reports of similar shell-seeking behaviors by marine hermit crabs in response to dead conspecific odors. It is suggested that responding to dead conspecific odors for shell source location is an evolutionarily conserved behavior developed before hermit crabs became terrestrial.

Keywords: Chemical cue; Land hermit crab; Marine hermit crab; Shell-acquisition behavior

1. Introduction

Shell acquisition is a vital behavior for hermit crabs. Shells are limited in many hermit crab environments, but are required for hermit crab survival and reproduction (Vance,

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1972; Abrams, 1978, 1980; Hazlett, 1981; Spight, 1985). Marine hermit crabs depend upon properly fitting shells for protection from predators and desiccation (Hazlett 1981), mating success (Hazlett, 1989), and maximum clutch size (Childress, 1972; Fotheringham, 1976; Wilbur, 1989). Larger shells are needed periodically as hermit crabs grow (Fotheringham, 1976; Hazlett, 1981).

Marine shell sources include dying gastropods and other hermit crabs (McLean, 1974, 1983; Rittschof, 1980a; Wilbur & Herrnkind, 1984). Marine hermit crabs locate dying gastropods and dying conspecifics at a distance by detecting odors generated by proteolytic activity on gastropod flesh (Rittschof, 1980b) and odors of hemolymph diffusing from wounded conspecifics (Rittschof et al., 1992). Efficient location of shell sources prevents loss of a shell to the hermit crab population by burial (Hazlett, 1981) or preemption by other shell users (McLean, 1983) and provides a focus for shell exchange activities (McLean, 1974; Chase et al., 1988; Rittschof et al., 1992).

Marine hermit crabs chemically attracted to shell sources display specific behaviors related to shell acquisition rather than to feeding (Rittschof, 1980a; Rittschof et al., 1992). Crabs attracted to shell sources do not feed and are unattracted to foods (Rittschof 1980a; Rittschof et al., 1992). Attracted crabs investigate other crabs' shells by touching them with their chelipeds and walking legs and inserting their legs and cephalothorax into the shell aperture (Rittschof, 1980a; Rittschof et al., 1992). Crabs aggregate around the dead animal with crabs of descending size hanging on to each others' shells (McLean, 1974; "scrum" Rittschof, 1980a; Rittschof et al., 1992). Lining up, or scrumming (Rittschof, 1980a) enables efficient transfer of shells among individuals: an initial crab discards its shell for the new shell and crabs of descending size move into available shells. Thus, several crabs move into larger shells with the introduction of a single shell (Rittschof, 1980a; Chase et al., 1988; Rittschof et al., 1992). Shell fit influences hermit crab behavior and response to shell cues: crabs in too small shells aggregate at shell cue odors while crabs in well-fitting shells withdraw or flee (Rittschof et al., 1992; Katz and Rittschof, 1993).

In agreement with previous reports of shell limitation in land hermit crabs, *Coenobita spp*, (Abrams, 1978), few empty shells and crabs were found in grossly too small, too large or broken shells (M. Small, R. Thacker, pers. obs.) and occasionally naked (R. Thacker, pers. obs.). Crabs were found using soy sauce caps (Chief Sakius George, pers. comm.) and shampoo bottle caps (R. Thacker, pers. obs.) as shell substitutes. It is suggested that shell limitation applies similar constraints on survival and fitness in *Coenobita spp.* as is the case for marine hermit crabs. Thus, shell source detection should be important for *Coenobita spp.*

Shell source detection and shell switching behavior was tested in two species of *Coenobita* in two tropical locations: *Coenobita perlatus* (H. Milne Edwards) at Kapingamarangi, Federated States of Micronesia (Kapinga, 1°N., 154°E) and *Coenobita compressus* (H. Milne Edwards) at Achotines Bay, Los Santos Province, Republic of Panama (Achotines, 7° 25′ N., 80° 10′ W.). *Coenobita* behaved similarly in both locations and showed behaviors previously reported for marine hermit crabs (Rittschof et al., 1992). *Coenobita* aggregated at dead conspecific odors and shell exchange cascades were observed when empty shells were provided. In contrast to marine hermit crabs, *Coenobita* fed in response to odors of dead snails (Thacker, in review). It is

suggested that locating dead conspecifics as a shell source is an evolutionarily conserved behavior, but chemical cues used to locate shells on land differ from marine shell cues.

2. Materials and methods

2.1. Study areas

The study at Kapinga atoll was conducted on Dahling, a coral reef islet, during December 1992. Dahling, roughly 5 acres in area, is covered by a dense forest of tropical trees. Tens of thousands of *Coenobita perlatus* are found near the sandy lagoon beach while larger *Coenobita brevimanus* (Dana) inhabit the forest. During cloudy days *Coenobita perlatus* foraged on beach wrack and on fallen *Pandanus sp.* fruit, coconut and detritus. *Coenobita perlatus* aggregated under materials in the wrack zone, on palm tree trunks, on the branches of low bushes and excavated and hid in small holes. On hot, clear days few crabs were active. *Coenobita brevimanus* were seen occasionally in the forest during the day but usually remained concealed among forest litter. *Coenobita brevimanus* came out at night and foraged in the same places as the smaller crabs and on similar foods. Experiments were conducted using only *Coenobita perlatus* between 0800 and 1100 and between 1500 and 1900.

Research at Achotines Bay was conducted at the Achotines Laboratory of the Inter-American Tropical Tuna Commission between January and March (dry season) of 1992 and 1993. The bay is bordered by a sand and rock beach, with tropical dry forest shading the beach until noon. *Coenobita compressus* are found on the beach and in the forest. Smaller crabs are active in mornings until the beach is no longer shaded. All sizes of crabs are active at night, with maximum activity during falling tides at dawn and dusk. Experiments at Achotines were performed in mornings between 0600 and 1030 and in evenings between 1730 and 1930.

2.2. Biological assays

In initial experiments on Kapinga and at Achotines, empty shells, dead conspecifics and food items were placed in arenas to observe *Coenobita* behavior. *Coenobita* attraction to odors and behavior stimulated by odors were then tested in a series of experiments: (1) an attraction assay (Kapinga); (2) a pit experiment assaying attraction and behavior using hidden odor sources and concealed empty shells in shallow pits (Kapinga and Achotines); and (3) a bucket experiment assaying behavior in buckets with odor sources and empty shells (Kapinga and Achotines).

2.3. Attraction assay

Coenobita perlatus responses to odors were observed by counting crabs attracted to different hidden odor sources on Kapinga. Odor sources were placed in 100 ml plastic beakers covered with fiberglass windowscreen. An empty covered beaker served as

a control. Beakers were buried flush with the sand 0.5 m apart in a straight line parallel to the water. Odor sources included 1 cm cubes of: *Pandanus sp.* fruit (often seen being eaten by crabs); frozen and thawed *Planaxis sulcatus* and *Nerita sp.* (high intertidal snails); frozen and thawed marine diogenid hermit crabs and frozen and thawed conspecifics. Crabs could neither see odor sources from a distance nor touch sources they found.

The experiment was installed in three sites on the beach two meters below the wrack zone and near fruit litter under a *Pandanus sp.* tree. Areas were intermittently traversed by crabs during the day. Crabs were randomly distributed on the beach and away from the fruit litter and clustered in the wrack zone and around fruit. Crabs were counted when they touched the screen over the odor source, then were removed to prevent double counting and to minimize social interaction (Rittschof & Sutherland, 1986). This assay was repeated seven times; the order of the beakers was changed each time. The numbers of crabs attracted to each odor source were tested with *G*-tests (Sokal & Rohlf, 1981) to examine the possible effects of location on trial results. Location results were then grouped and compared with a χ^2-test (Sokal & Rohlf, 1981) to determine differences in odor attractiveness.

2.4. Pit experiments

In this assay, shell acquisition behavior was observed at odor sources concealed within shallow pits. At Kapinga, odor beakers were constructed as in the attraction assay and set in the center of sand pits (6 cm deep, 60 cm diameter) on the beach with a clean empty shell hidden under the lip of each beaker. This arrangement controlled for social attraction and attraction by the sight of an empty shell (Reese, 1963; Elwood & Stewart, 1985). Pits were aligned 1.2 m apart near crab feeding sites. Beakers containing either *Pandanus* fruit, *Nerita* or a dead conspecific were rearranged for each of six trials. Arriving crabs were counted (but not removed since individuals were recognizable) and shell switches noted. If subsequent crabs switched into the abandoned shell during a trial, the action was termed a sequential cascade (of shell switches). Numbers of crabs arriving at different odors were compared with a χ^2-test (Sokal & Rohlf, 1981). Proportions of crabs switching shells and numbers of cascades were compared among the different odor sources with *G*-tests (Sokal & Rohlf, 1981). Significant values were further examined with pairwise comparisons (Sokal & Rohlf, 1981).

At Achotines, the pit experiment was installed on a beach site intermittently traversed by crabs. Odor sources were placed in small sand pits (5 cm deep, 5 cm diameter) covered with fiberglass screening, within larger sand pits (5 cm deep, 60 cm diameter), with a clean empty shell at the edge of the interior odor pit. Odor sources used were: control, *Bombacopsis sessilis* flowers (flowers from this tree were often eaten by hermit crabs), *Nerita scabricosta* (intertidal snail), *Ocypode gaudichaudii* (H. Milne Edwards and Lucas, a terrestrial brachyuran crab), *Calcinus obscurus* (marine hermit crab) and *Coenobita compressus*. All odor sources were collected fresh and crushed to facilitate the release of odors immediately prior to each trial. The assay was repeated five times. In the first 4 min after the first crabs arrived at a pit, the number of crabs attracted to each odor and the number exhibiting fondling behavior (touching other crabs' shells in

an exploratory manner) were recorded. The assay continued for another 6 min and total numbers attracted during 10 min and number of shell switches in 10 min were recorded. Large numbers of arriving crabs prevented reliable fondling observations after 4 min. Trial data were tested for differences among trials with *G*-tests (Sokal & Rohlf, 1981). Proportions of crabs fondling at each odor source were compared with a *G*-test (Sokal & Rohlf, 1981). Total numbers of crabs attracted to each odor source by 4 and 10 min were compared with χ^2-tests (Sokal & Rohlf, 1981). Proportions of shell switches and cascades at different odor sources were compared with *G*-tests (Sokal & Rohlf, 1981). Significant effects were examined with post hoc pairwise comparisons, adjusting critical values for the number of comparisons made (Sokal & Rohlf, 1981).

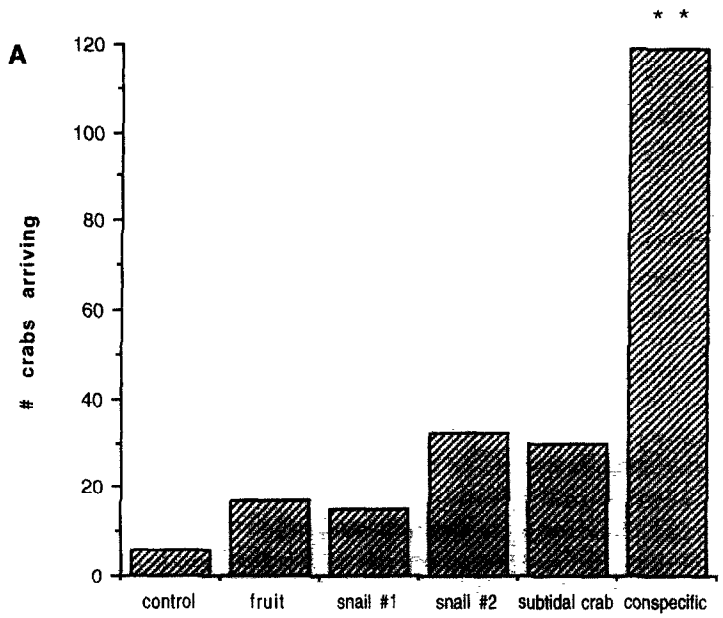
2.5. *Bucket experiments*

Three categories of crabs were identified at both study locations: feeding crabs, crabs eating *Pandanus* fruit (Kapinga) or *B. sessilis* flowers (Achotines); scrumming crabs, crabs from a scrum around a dead conspecific (Kapinga and Achotines); and random crabs, crabs walking in the area, and selected haphazardly (Kapinga and Achotines). It was thought that shell switching behavior might differ among these crab categories. It was hypothesized that feeding crabs would switch less than crabs seeking shells (scrumming crabs attracted to dead conspecific odors) and that random crabs should switch at an intermediate frequency.

Bucket experiments (Rittschof et al., 1992) were used to explore behavioral differences among the crab categories, and to test the possibility that shell switching behaviors are stimulated by dead conspecific odors. First, 10 crabs from a single category were observed for 3 min in a clean 2 gallon bucket. Then, a dead conspecific was added and crab behavior was observed another three min. Finally, a clean, unoccupied shell was added and crab behavior was observed another 15 min. If more than one crab switched into a new shell, the action was termed a cascade. At Kapinga, this experiment was repeated three times each with random crabs and feeding crabs and four times with scrumming crabs. Time constraints prevented more trials. At Achotines, this experiment was repeated five times each with random crabs, feeding crabs and scrumming crabs. Fresh crabs were always selected for each trial. The numbers of shell switches among crabs from different categories were compared with *G*-tests (Sokal & Rohlf, 1981). The numbers of cascades among crabs from different categories were compared with Fisher's Exact Tests (Sokal & Rohlf, 1981).

2.6. *Second achotines bucket experiment*

A second bucket experiment conducted at Achotines controlled for behavior possibly stimulated by food odors and empty shells and examined the behavior of crabs found aggregated for unknown reasons. Trials followed the same format of placing 10 crabs in a bucket, adding an odor source and then an empty shell. Crabs were selected from a single category: random, feeders, scrummers, and also aggregates (crabs aggregated for unknown reasons). Odor sources included a control (no odor), food (*B. sessilis* flowers), and dead conspecific. Each crab category was tested in five trials with each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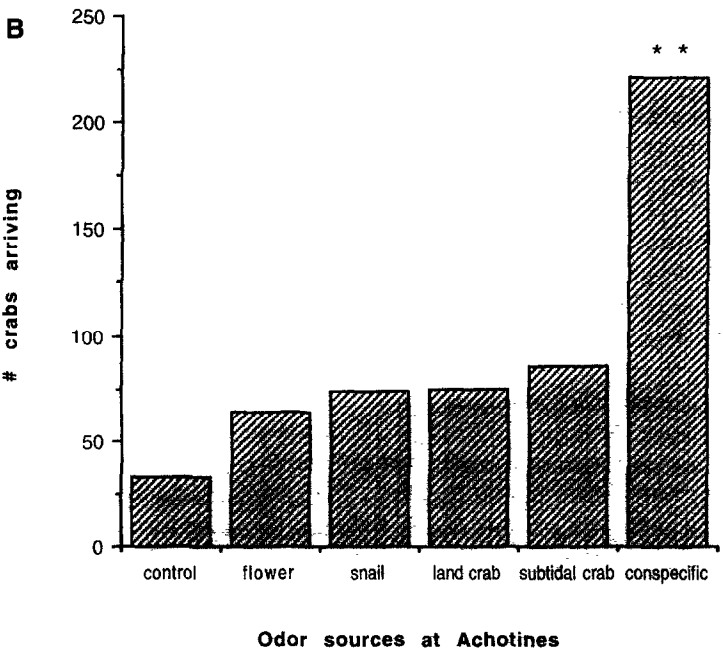
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of the three odors for a total of 15 trials per category. *G*-tests (Sokal & Rohlf, 1981) were conducted to determine if responses to odors were independent of crab categories. Subsequently, separate *G*-tests (Sokal & Rohlf, 1981) were conducted to examine the effect of crab categories and odor sources on the number of exchanges and cascades. Significant effects were examined with post hoc pairwise comparisons, adjusting critical values for the number of comparisons made (Sokal & Rohlf, 1981).

3. Results

3.1. Initial observations

During initial experiments at Kapinga and Achotines, clean empty shells were unattractive at a distance but explored if a crab walked by. Dead conspecifics placed in an arena attracted up to 100 crabs from up to 10 m during 20-min trials. Behavior was interpreted as shell-seeking: crabs did not eat dead crabs, but investigated shells of other crabs and were observed to form scrums. If an unoccupied shell was provided, a cascade occurred.

3.2. Odor attraction in the Kapinga attraction assay and Achotines pit experiment

Results for odor attraction were similar in Kapinga and Achotines experiments. Odor sources attracted significantly more crabs than did the control ($p<0.01$, Kapinga, Fig. 1a; $p<0.01$, Achotines, Fig. 1b). Odor sources differed from each other in attractiveness: dead conspecifics attracted more crabs after 10 min in both Kapinga and Achotines experiments ($p<0.01$, Kapinga, Fig. 1a; $p<0.01$, Achotines, Fig. 1b). At Achotines, the snail, marine hermit crab and ghost crab were indistinguishable from the *B. sessilis* flower in attractiveness. In pairwise comparisons of Kapinga data, conspecifics were more attractive than each other odor source (all p-values <0.01). On day 1 of attraction trials on Kapinga, the snails and diogenid hermit crab were indistinguishable in attractiveness from *Pandanus* fruit. When the same *P. sulcatus* and diogenid crab were used again on day 2, their attractiveness was more than the freshly thawed *Nerita sp.* or *Pandanus* fruit ($p<0.05$).

3.3. Attraction to odors and fondling in Achotines pit experiment

In the first 4 min of the Achotines pit experiment, odor sources differed significantly in the number of crabs attracted ($p<0.01$, Fig. 2). Pairwise comparisons found dead

Fig. 1. Number of *Coenobita sp.* attracted to hidden odors on Kapinga (A) and Achotines (B). During 10-min trials crabs going to each hidden odor were counted. Odor sources on Kapinga included: control = empty beaker; fruit = chunk of *Pandanus sp.* fruit; snail #1 = dead *Nerita sp.*; snail #2 = dead *Planaxis sulcatus*; marine crab = dead diogenid hermit crab; conspecific = dead *Coenobita perlatus*. Odor sources in the Achotines experiment included: control = empty beaker; flower = *B. sessilis*; snail = dead *Nerita scabricosta*; land crab = dead *Ocypode gaudichaudii* (ghost crab); marine crab = dead *Calcinus obscurus*; and conspecific = dead *Coenobita compressus* Categories were tested with *G*-tests significant results are marked with * for $p<0.05$, and ** for $p<0.01$.

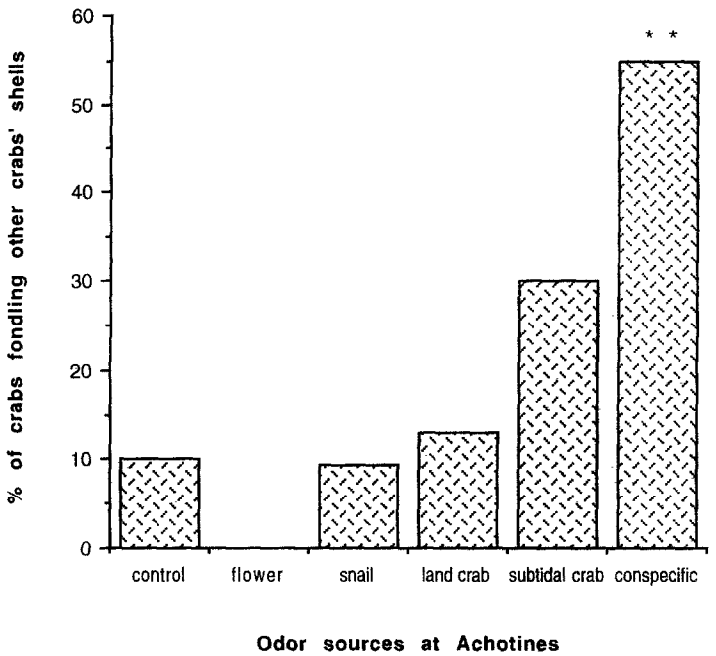


Fig. 2. Frequency of *Coenobita compressus* exploring other crabs shells (fondling) in the first 4 min of pit experiment at Achotines. Odor sources include: control = empty beaker; flower = *B. sessilis*; snail = dead *Nerita scabricosta*; land crab = dead *Ocypode gaudichaudii* (ghost crab); marine crab = dead *Calcinus obscurus*; and conspecific = dead *Coenobita compressus*. Categories were tested with *G*-tests, significant results are marked with * for $p<0.05$, and ** for $p<0.01$.

conspecific odor significantly more attractive than *B. sessilis* flower odor ($p<0.05$) and control ($p<0.01$). A significantly higher proportion of crabs attracted to a dead conspecific or a marine crab exhibited fondling behavior than did crabs attracted to other odor sources ($p<0.01$, Fig. 2; multiple comparisons $p<0.01$).

3.4. *Switching and cascading in pit experiments*

In the Kapinga pit experiments, crabs approached pit rims, appeared to look into the pit, then climbed down the slope. Some crabs circled the rim before entering. Slopes were gentle enough for easy access yet visually concealed activity within pits. When crabs switched shells, they entered the pit, went to the odor source, explored around the odor source, found and explored the shell, switched if it was bigger than their shell, then immediately left the pit. Rittschof (1980a) observed similar behavior in marine hermit crabs. Some crabs switched into relatively large shells. At Kapinga, 10 times more crabs attended dead crab pits than pits with other odors ($p<0.01$). Switching frequency was similar at conspecific, fruit and control odors and lower at the nerite odor ($p<0.05$). Shell switching cascades only occurred at conspecific odor ($p<0.01$) and stopped when the last shell discarded was in poor condition (holes, breakage, etc.) or too small for attending crabs.

In Achotines pit experiments, switching occurred at all odors at similar frequencies ($p > 0.05$). More cascades followed a switch at the conspecific odor than at other animal odors ($p < 0.05$) and no cascades occurred at the flower and control sites.

3.5. *Bucket experiments*

Behavior differed among crab collection categories in the bucket experiment. On Kapinga, crabs from the random and feeding categories moved around during the initial 3 min with limited exploration of other crabs' shells. After introducing a dead crab, moving continued. When an empty shell was added, a switch usually occurred but was never followed by a cascade (Fig. 3a). Scrumming crabs reformed scrums in the initial 3 min, switched shells when the empty shell was added ($p < 0.05$ Fig. 3a) and always cascaded ($p < 0.05$, Fig. 3a).

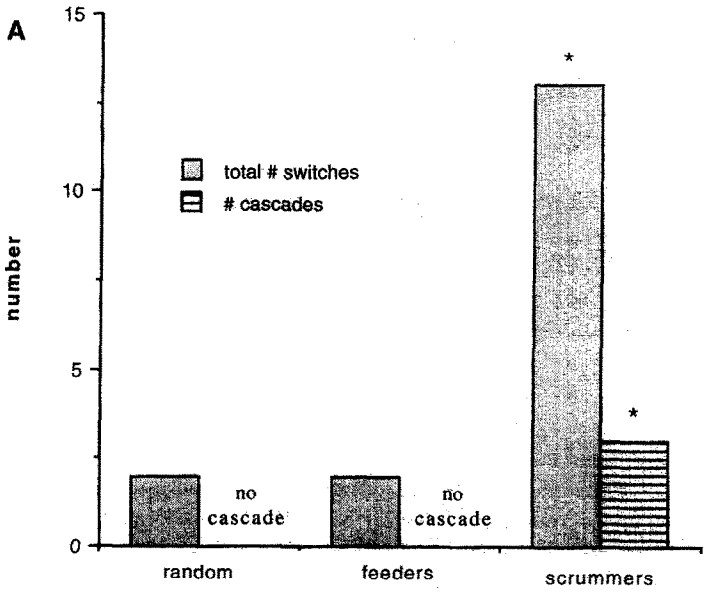
In Achotines bucket experiments, crabs in each category switched into new shells. Crabs attracted to dead conspecifics switched more than crabs collected randomly and around food ($p < 0.05$, Fig. 3b). Shell switches were sometimes followed by cascades with scrumming crabs and with randomly collected crabs (Fig. 3b). Feeding crabs did not cascade after shell switches (Fig. 3b). This difference in cascades among crab categories was statistically insignificant.

3.6. *Effects of attracting odors and stimulus odors*

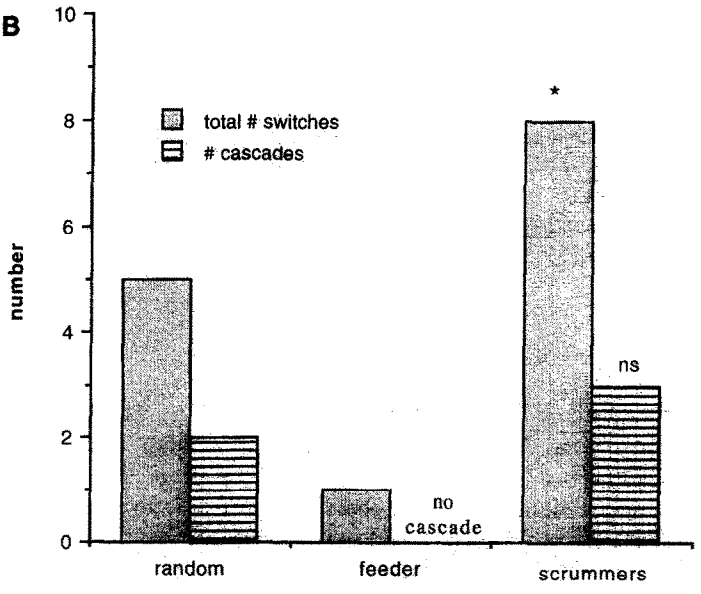
In tests determining if crab attraction categories and odor stimuli influenced switching and cascading, crabs from all four categories switched shells (Fig. 4) and cascaded. Numbers of crabs switching in different crab categories was independent of odor source (Fig. 4). Odor source had no significant effect on switching (Fig. 4), but switching did vary significantly among crab categories ($p < 0.05$, Fig. 4), with significantly more crabs attracted to dead conspecific switching shells than crabs attracted to *B. sessilis* flowers ($p < 0.01$). The numbers of crabs cascading in different categories was independent of odor source. Different odor sources had insignificant effects on the number of cascades, but the number of cascades differed significantly between crab categories ($p < 0.05$), with more crabs attracted to dead conspecifics cascading than crabs attracted to flowers ($p < 0.05$).

4. Discussion

Land hermit crabs from two locations behave similarly to each other and to marine hermit crabs in response to odors of dead conspecifics. Both land and marine hermit crabs are preferentially attracted to odors of dead conspecifics and display behaviors related to shell acquisition rather than feeding. Attracted crabs routinely locate and switch into shells, do not eat the dead crab and flee after switching. "Chemically primed" aggregated land crabs switch shells as found in aggregated marine hermit crabs (Rittschof 1980a). Land hermit crabs differ from marine crabs in responses to odors of dead snails. Marine hermit crabs aggregate around dead and dying snails and ex-



Categories of crabs on Kapinga



Categories of crabs at Achotines

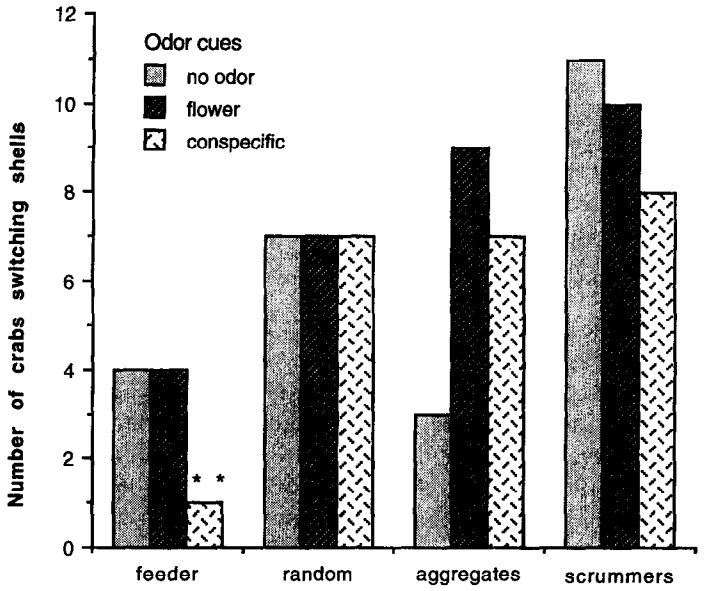


Fig. 4. Shell switching in second Achotines bucket experiment. Crabs were put in a bucket with an odor source and an unoccupied shell. Crabs from different categories were gathered and tested separately: feeder = crabs feeding on *B. sessilis* flower; random = crabs walking around and collected haphazardly; aggregates = crabs found aggregated for unknown reasons; conspecific = crabs attracted to dead conspecific odors. Crabs from the different categories were tested for shell switching behavior in the presence of different odors: no odor; flower (*B. sessilis*) and dead conspecific. Switching in different categories with different odors was tested with *G*-tests. Significant differences are marked with * for $p < 0.05$ or ** for $p < 0.01$.

change shells when the new shell becomes available (McLean, 1974; Rittschof, 1980a); dead snail odors attract *Coenobita* only as much as other foods. Snail odors do not preferentially attract crabs in search of new shells (Thacker, in review; Rittschof & Sutherland, 1986).

The different physical properties of air and water prescribe the chemistry of shell source signaling over distances. Marine chemical cues can be non-volatile or volatile since both may be sufficiently soluble in water (Rittschof, pers. comm.), but terrestrial cues must be volatile (Rittschof & Sutherland, 1986). Soluble shell cues emitted from marine crab hemolymph are small enough to be volatile (Rittschof et al., 1992) but their specific nature is unknown. Shell cues from *Coenobita sp.* hemolymph are volatile and the possibility of a soluble fraction will be tested in a future experiment. Both cues act

Fig. 3. Shell switches and cascades in the first bucket experiments on Kapinga and at Achotines. Crabs were put in a bucket with a dead conspecific and an unoccupied shell. Crabs from different categories were gathered and tested separately: random = crabs walking in area and selected haphazardly; feeders = crabs feeding on *Pandanus sp.* fruit on Kapinga and *B. sessilis* flowers at Achotines; conspecific = crabs aggregated at dead conspecific odors. In a switch, a crab moved into the unoccupied shell. In a cascade, crabs moved into discarded shells. Results were tested with *G*-tests: * marks *p*-values < 0.05.

quickly upon release and elicit similar behaviors in crabs seeking shells (aggregation, fondling other crabs' shells, scrum formation and shell switching). These similarities may result from at least three possibilities: (1) locating dead conspecifics as a shell source is a conserved behavior and the chemical cues may have similar molecular origins, (2) the convergent behavior evolved separately and is cued by different chemicals and (3) the behavior is learned. The first explanation is favored.

Marine and land hermit crabs respond differently to snail flesh odors. Wounded snails release a non-volatile peptide cue which attracts shell-seeking marine crabs within minutes (Rittschof, 1980b; Rittschof et al., 1990; Kratt & Rittschof, 1991). The snail cue mediates shell-seeking behaviors (Rittschof, 1980a,b) similar to those descibed in response to conspecific cue (Rittschof et al., 1992). Juvenile *Coenobita compressus* in an aqueous environment respond to shell cues from snail flesh similarly to marine hermit crabs (Gilchrist, 1991). However, on land adult *Coenobita spp.* respond to snail flesh odor only as carrion, not as a shell cue (Rittschof & Sutherland, 1986; Thacker, in review, this study). Over time, decomposing marine snail flesh also attracts scavenging crabs (Rittschof, 1980a). Snails thus release two cues, a non-volatile peptide shell cue and decomposition products signaling carrion, some of which are volatile. Adult land crabs respond to volatile carrion cues, supporting Gilchrist's (1991) hypothesis that antennal receptors change with ontogeny and emergence onto land. Future experiments will test land crab responses to soluble shell cues.

Hermit crab responses to food odors and their hierarchy of decisions may be influenced by shell fit in different environments. Under experimental conditions, Rittschof (1980a; et al., 1992) and Gilchrist and Abele (1984) found marine hermit crabs responding to shell cues did not eat and potential foods were unattractive. Marine hermit crabs in poorly fitting shells aggregate at shell odor sources and switch into available shells while crabs in well-fitting shells flee or withdraw (Rittschof et al., 1992; Katz & Rittschof, 1993). Marine hermit crab studies have shown that behavioral responses to food odors or shell cues depend upon shell fit (Elwood & Stewart 1985; Neil & Elwood, 1986; Rittschof et al., 1992; Katz & Rittschof, 1993). In this study *Coenobita* attracted to food odors displayed few shell exchange behaviors. It was hypothesize that land hermit crabs attracted to food odors are in better fitting shells and that crabs attracted to dead conspecific odors are in worse fitting shells.

Shell source location and switching is controlled by interactions of chemical and visual cues. When stimulated by snail flesh odors, the intertidal hermit crab, *Clibanarius vittatus* (Bosc), responds to visual stimuli in a manner consistent with shell seeking behavior (Orihuela et al., 1992). *Coenobita* locate shells visually (Reese, 1963). In our preliminary tests, an empty shell with no dead crab was only taken if a crab encountered it by chance. In the second Achotines bucket experiment crabs were tested for switching behavior with just a shell or with a shell and odors. Crabs from all categories switched into offered shells regardless of odor present. In both Kapinga and Achotines pit experiments, even though more crabs attended dead conspecific odor, similar percentages of crabs switched into new shells at most odor sources and controls. Thus, crabs finding an empty shell were equally likely to switch regardless of the attracting cue. These results, together with attraction to odors in the other experiments, suggest that land hermit crabs use volatile odors of conspecifics to detect shell sources

from a distance then locally find shells visually. Detecting shell sources with odors rather than with sight enables *Coenobita* to find shells at night when they are more active, an important strategy for locating shells efficiently.

Detecting and aggregating at dead conspecific odors enables effective acquisition of larger shells (Rittschof et al., 1992; Katz & Rittschof, 1993) from either a dead conspecific or as a discard from another crab. Once a crab switches into the vacant shell, its discarded shell is taken by a smaller crab and the process continues until the discarded shell is of poor quality or smaller than assembled crabs. While initially only one shell is available, the majority of crabs receive new shells by exchanging in the cascade or "vacancy chain" (Chase et al., 1988). Thus, several crabs benefit by aggregating at an odor source associated with a vacated shell.

Five species of marine hermit crab (Rittschof et al., 1992; *Calcinus tibricen* and *Calcinus sewati,* Hazlett, pers. comm.) and at least two species of land hermit crab use conspecific odors to locate new shells. It is suggested that this is an evolutionarily conserved behavior which developed before hermit crabs became terrestrial. It is speculateed that other hermit crab species also use dead conspecific odors to locate shells.

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