Shell and food acquisition behaviors: Evidence for Contextual Decision Hierarchies in hermit crabs

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ABSTRACT

Shell and food acquisition behaviors of the hermit crab, *Pagurus samuelis*, were examined in response to cues of shell and food availability. Tactile, visual, and chemical cues were presented in a factorial manner, and time was measured between initial contact and either inhabitation of a shell or initiation of feeding. We considered the time difference between initial contact and subsequent behavior to be a measure of hermit crab 'decision time'. For shell acquisition experiments, treatments that included tactile cues elicited significantly shorter decision times (8.5–117.1 s), than treatments without tactile cues (294.5–765.2 s). In contrast to the shell acquisition experiment, we found that in food acquisition experiments, treatments that included chemical cues elicited significantly shorter decision times (78.4–450.5 s), than those without chemical cues (570.0–778.1 s). Although primary cues elicited the shortest decision times during foraging and shell-seeking, in the absence of the primary cue, secondary cues could still be used to make appropriate decisions, albeit with significantly longer decision times. Therefore we propose that hermit crabs sort environmental information in 'Contextual Decision Hierarchies' in order to make accurate and efficient behavioral choices.

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1. Introduction

In many cases, behaviors exhibited by animals are not merely reflexes to specific stimuli, but rather decisions that are mediated by available information and modulated by internal physical state or motivation (Neil, 1985; Shettleworth, 2001; Fahrbach and Mesce, 2005; Billock and Dunbar, 2009). Hermit crabs make an ideal model system for studying sensory capabilities and decision-making processes in crustaceans because their shelters, food sources, and mates, may all potentially have the same appearance. This may necessitate the adaptation of behavioral and physiological means to differentiate between resources. To make efficient use of information, it must be sorted and prioritized.

There is evidence that behavioral cues are arranged hierarchically. In the hermit crab *Pagurus longicarpus*, reaction to cues of a familiar conspecific varied in intensity with 'sight and smell' eliciting the strongest response, 'smell only' eliciting a response, and 'sight only' eliciting no significant response (Gherardi and Tiedemann, 2004). There is also evidence that animals may shift to a secondary cue when the primary cue is unavailable. For the fiddler crab, *Uca cumulanta*, sun position was the primary cue during homing behavior, but on cloudy days the secondary cues of beach slope or landscape profile could be utilized to determine homeward direction (Chiussi and Diaz, 2001). The hermit crab, *Pagurus longicarpus*, prefers to use celestial cues for migration on sunny days, but will switch to substrate slope information on cloudy days (Rebach, 1978, 1981).

In making resource acquisition decisions, visual, chemical, and tactile information may be utilized differently based on motivation. Elwood (1995) found that if a hermit crab is strongly motivated to acquire a better shell, it will make decisions more rapidly, work harder to obtain a shell, and will be less distracted by signals of danger. Neil (1985) found that while hermit crabs in inadequate shells are highly motivated to acquire an adequate shell, being smaller than the opponent or having a missing or regenerating major cheliped can reduce motivation. Land hermit crabs in inadequate shells were attracted to the odor of dead conspecifics while crabs in adequate shells were more attracted to the odor of food (Thacker, 1994). In addition, Billock and Dunbar (2009) found that hermit crabs specifically seek resources of which they have been deprived. This implies that hermit crabs take into account their current needs when making decisions, and that motivation influences behavior. Little work has previously been done to test the capacity for decision-making in lower trophic crustaceans. In nature, hermit crabs encounter objects that may have visual, chemical, or tactile cues that mimic the characteristics of available shells or food. It may be important for them to be able to distinguish actual shelter and food from the myriad of other objects in tide pools that, despite their similarity in texture, shape, or color, are merely decoys. This study investigated whether hermit crabs sort incoming information about their environment in order to make decisions quickly and efficiently. Our aim in this study was to investigate which stimuli take priority in eliciting shell acquisition and food acquisition behaviors, and to what

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degree decision-making changes when the available information is altered.

In this study, it is our premise that the relative value of a stimulus in eliciting a behavioral response depends upon context. As animals process information about their environment, some cues elicit stronger responses than others. We define "Contextual Decision Hierarchies" (CDH) as the relative weighting of external information based on internal and external contexts. Internal contexts are defined by motivation, such as the need for food, while external contexts are defined by the environment, such as darkness or the presence of a predator. Our first hypothesis was that when faced with the internal context of needing a resource (shells or food), hermit crabs would utilize a CDH such that they would demonstrate a rank-order preference among visual, chemical, and tactile stimuli when acquiring a resource. Our second hypothesis was that the CDH employed by hermit crabs depended upon which resource was being sought, such that the stimulus that had the largest influence on shell acquisition behavior would be different than the major stimulus that influenced food acquisition.

2. Methods

2.1. Animal collection and maintenance

The blueband hermit crab, *Pagurus samuelis*, and the black turban snail, *Tegula funebralis*, were collected from Little Corona del Mar, Newport Beach, California (33°35.36′N, 117°52.09′W) in June and August, 2006, and February, 2007. Crabs were divided evenly between two aquaria and maintained separately in 5 cm D × 7 cm H polyvinylchloride (PVC) cylinders. All animals were maintained at $24 \pm 1.0\,°$C with ambient natural light. For the shell acquisition experiment, hermit crabs were fed Crab & Lobster Bites (HBH Pet Products, Springville, Utah) three times per week. For the food acquisition experiment, hermit crabs were fed only once per week, and starved from 4 to 7 days prior to testing.

Prior to testing, each hermit crab was measured for total wet weight (including shell), shell aperture width, and length. After removal from the shell, crab body weight and carapace length were also measured. These measurements were used to determine the preferred shell size for each individual. Body weight of *P. samuelis* can be used to predict the preferred shell aperture width (Billock and Dunbar, 2009).

2.2. Shell acquisition

Hermit crabs were tested in a circular arena with a *T. funebralis* shell and four decoy objects that were similar in size, shape, texture, and/or color to the target shell. As seen in Fig. 1, the decoys used were: a black rubber stopper 12 mm in height (color and shape similarity); a smooth pebble 15 mm in height (color and shape similarity); a round piece of clear glass 11 mm in height (shape similarity); and a small, flat piece of bivalve shell 22 mm wide and 0.2 mm in height (texture similarity). The *T. funebralis* shells ranged in size from 13 to 23 mm in height.

During test sessions, visual, chemical, and tactile cues of shell availability were presented in a factorial manner (see Table 1): no added visual, chemical, or tactile cues (NonVCT); visual (V); chemical (C); tactile (T); visual–chemical (VC); visual–tactile (VT); chemical–tactile (CT); and visual–chemical–tactile (VCT). During visual treatments, light was provided by an artificial, full-spectrum sunlight bulb. For non-visual treatments, the arena was dark, yet hermit crab movement could easily be viewed via an infrared camera. For the purposes of this study, we defined "chemical cues" as water-borne odor molecules that were detected without physical contact with the emitting agent, primarily detected by the antennae. We defined "tactile cues" as information gleaned while in contact with the object
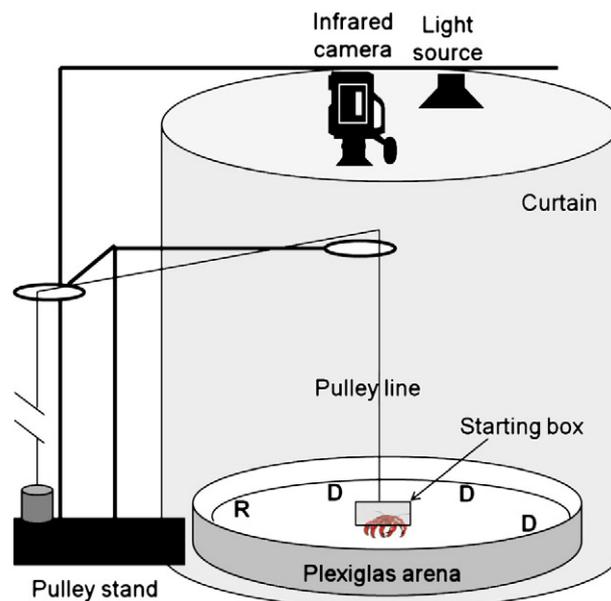

Fig. 1. Diagram of test arena showing Plexiglas arena, hermit crab starting box, object placement, and pulley system. Object locations are represented by letters: food or shell resource (R) and decoy objects (D). Diagram is not to scale.

by either the chelipeds or walking legs. Tactile information is obtained through both chemoreceptors (detecting calcium and other molecules) and proprioceptors (detecting texture, size, and weight) (Mesce, 1982, 1993a). For chemical treatments, seawater was infused with odor of recently killed *T. funebralis*. The snail was placed in a freezer for 1 h and then crushed in a vice to break open the shell. The flesh was removed with tweezers and weighed. The snail flesh was cut into small pieces with a scalpel and 1.0 ± 0.1 g was added to 4.0 l of seawater. After 1 h, the solution was filtered to remove any particulate matter. During tactile treatments, a clean *T. funebralis* shell was placed in the arena, and for the non-tactile treatment a wax coated shell was used (Mesce, 1993b). A thin, clear wax coating was applied by dipping shells in melted, unscented candle wax. Shell aperture widths were measured and each crab was offered a test shell that was within 1.25 mm of its preferred shell aperture width, as measured before the experiment began.

Eight replicates were conducted for each treatment, and each treatment was repeated four times (N = 32). Stimuli were presented in random order to the subjects for each test, and each animal was tested only once per day. The arena was filled with 550 ml of seawater

Table 1

Factorial treatment organization for shell and food acquisition experiments. Visual and tactile cues were the same in both experiments, while chemical cues differed between the two. In the shell acquisition experiment, the chemical cue was provided by the type of seawater that filled the arena. In the food acquisition experiment, the chemical cue was the odor emanating from the *T. funebralis* placed in the arena. Symbols: NonVCT = no added Visual, Chemical, or Tactile; V = Visual; C = Chemical; T = Tactile; VC = Visual + Chemical; VT = Visual + Tactile; CT = Chemical + Tactile; VCT = Visual, Chemical and Tactile.

	Visual cue	Tactile cue	Chemical cue	
Stimuli	Lighting	*Tegula* shell	Water (shell acq.)	Aperture (food acq.)
NonVCT	Dark (infrared)	Wax coated	Seawater	Wax sealed
V	Full spectrum	Wax coated	Seawater	Wax sealed
C	Dark (infrared)	Wax coated	*Tegula* seawater	Foot exposed
T	Dark (infrared)	Natural	Seawater	Wax sealed
VC	Full spectrum	Wax coated	*Tegula* seawater	Foot exposed
VT	Full spectrum	Natural	Seawater	Wax sealed
CT	Dark (infrared)	Natural	*Tegula* seawater	Foot exposed
VCT	Full spectrum	Natural	*Tegula* seawater	Foot exposed

or *Tegula* solution with the five test objects placed in random order around the border 1.5 cm from the edge. Hermit crabs were removed from their shells using a table vise. Each hermit crab was placed under a plastic box (2 cm × 2 cm × 1.5 cm) until the test began at which time the box was gently lifted by a pulley system. When the box was lifted, we recorded the time to first contact with the shell; number of contacts with the shell; and the total time elapsed before insertion into the shell. A maximum of 15 min per session was allotted. Hermit crabs that never made initial contact with the shell scored 15 min for "Initial Contact Time." If the hermit crab never inserted into the shell, the "Decision Time" was scored as 15 min.

2.3. Food acquisition

Procedures for the food acquisition experiment were the same as the shell acquisition experiment, except instead of using an empty *T. funebralis* shell, a freshly killed whole snail was used. Prior to testing, hermit crabs were given access to empty shells so they could choose their preferred shell. During the food acquisition experiment they were left in their shells. To minimize the number of snails that were sacrificed, each snail was used with eight crabs in a single treatment regime. The test snail was killed by freezing for 24 h. Prior to testing, the snail was thawed and the operculum removed. For chemical treatments, the foot muscle of a *T. funebralis* was left exposed, while for the non-chemical treatments, the shell aperture was filled with a drop of melted, unscented candle wax that when dry, was level with the rim of the aperture. The arena was filled with 550 ml of seawater in all treatments. For tactile stimuli, the exterior of the shell was left uncovered, while for the non-tactile cue, the exterior of the shell was coated with unscented candle wax by rapidly dipping once in a pool of melted wax. For both the shell coating and aperture filling, we visually inspected that no shell surface or foot muscle was exposed. Visual, chemical, and tactile cues were offered in the same combinations as shell acquisition tests (see Table 1). Eight replicates were conducted for each treatment, and each treatment was repeated five times (N = 40).

All experiments were conducted in a room with no external light source; however, we used green light near the video monitor to take notes. A black curtain surrounded the test arena to prevent any ambient light from entering the arena. The test arena was a 21.5 cm diameter clear acrylic cylinder covered in white Mylar to make it opaque (Fig. 1). All hermit crab movements were observed through a video monitor attached to a Nightview digital night vision camera with infrared illuminator (Weaver Optics, Meade Instruments Corporation, California). During visual treatment sessions, light was provided by a Philips brand 40 Watt "Natural Light," full-spectrum bulb that was suspended 75 cm above the test arena. Between each test, the arena and all test objects were rinsed with soapy water to eliminate potential odors from prior hermit crabs, and *Tegula* shells were rinsed in seawater or resealed with wax depending on treatment.

2.4. Statistical analysis

All statistical analyses were run using the Statistical Package for the Social Sciences (SPSS) 12.0 and 13.0. One-way repeated measures ANOVAs were conducted to determine differences in mean time to initial contact with the shell, mean number of shell contacts, and mean 'decision time' (time between initial contact and either inserting into the shell, for shell acquisition, or initiation of feeding, for food acquisition). Both initial contact time with the shell and decision time were not normally distributed, so data were rank transformed prior to running ANOVAs. Results were confirmed with Kruskal–Wallis tests.

3. Results

3.1. Shell acquisition

Although hermit crabs were housed in two different aquaria placed on the same lab bench, there was no significant difference between tanks in hermit crab mean decision time ($F_{1,242} = 0.063$, p = 0.802); therefore, data from both sets were pooled. Five hermit crabs died during the course of the experiment, resulting in a total sample size of 27.

A Kruskal–Wallis analysis revealed no significant differences among treatments in the mean time to initial contact with shells ($\chi^2 = 8.84$, df = 7, p = 0.264, see Fig. 2).

The mean number of contacts each hermit crab made with the shell per session was significantly different among treatments ($F_{7,182} = 21.64$, p < 0.001, partial $\eta^2 = 0.454$, see Fig. 3). Hermit crabs made significantly fewer contacts with the shell during treatments that included the tactile cue (T, VT, CT, and VCT), than they did in treatments that excluded tactile information. There was no significant difference among NonVCT, V, C, and VC treatments in number of contacts.

We considered the amount of time between when a hermit crab first contacted the shell and when it inserted its abdomen into the shell a measure of "decision time" to accept the shell. The difference among treatments in decision time was significant ($F_{7,182} = 35.93$, p < 0.001, partial $\eta^2 = 0.580$, see Fig. 2). Treatments that included the tactile cue (T, VT, CT, and VCT) had the lowest mean decision times. The VCT treatment elicited a significantly lower decision time than any of the other treatments. Alone, the V and C treatments were not significantly different from non-VCT in decision time; however, when combined in the VC treatment, these cues elicited a significantly shorter decision time.

3.2. Food acquisition

We tested two groups of hermit crabs; the first having 24 individuals and the second 16. There was no significant difference between groups in mean decision time ($F_{7,272} = 1.30$, p = 0.252); therefore, the data from both sets were pooled. Four hermit crabs died during the tests, resulting in a total sample size of 36 hermit crabs.
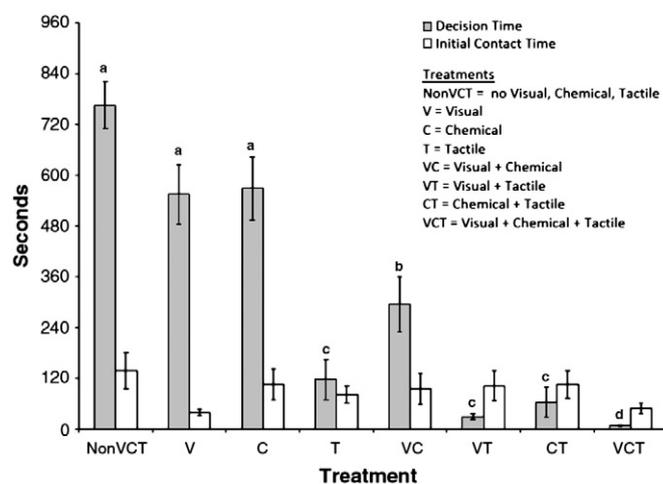

Fig. 2. The mean initial contact time and mean decision time during shell acquisition treatments. The maximum time per session was 900 s. Treatments with the same letter represent those with no significant differences among them in decision time. Error bars represent ± 1.0 SE. Reduced decision times indicate faster shell recognition. For comparison, the initial contact time for each treatment is indicated with unshaded bars. However, there were no significant differences among treatments (p > 0.05).
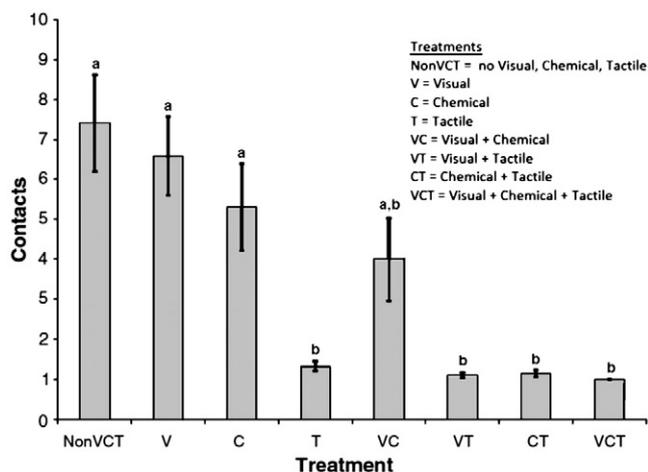
Fig. 3. The mean number of shell contacts during shell acquisition treatments. Treatments with the same letter represent those with no significant differences among them. Error bars represent ± 1.0 SE. Reduced number of contacts indicates faster shell recognition.

A Kruskal–Wallis analysis of initial contact time revealed no significant differences among treatments ($\chi^2 = 12.11$, df = 7, p = 0.097, see Fig. 4).

The mean number of contacts with the shell was significantly different among treatments ($\chi^2 = 53.74$, df = 7, p < 0.001, see Fig. 5). Hermit crabs made significantly fewer contacts with the gastropod when the chemical cue of gastropod odor was present, than when it was absent. Hermit crabs made the fewest contacts with the gastropod before deciding to feed, when both the chemical and tactile cues were present (CT and VCT treatments), although these treatments were not significantly different from VC or C.

Feeding decision time was calculated as the time difference between initial contact with the gastropod and the initiation of feeding. In treatments where the shell aperture was sealed with wax, hermit crabs in shells were scored as "feeding" when they stereotypically picked the wax from the aperture or when they pried the wax out and actually fed on the foot muscle beneath the
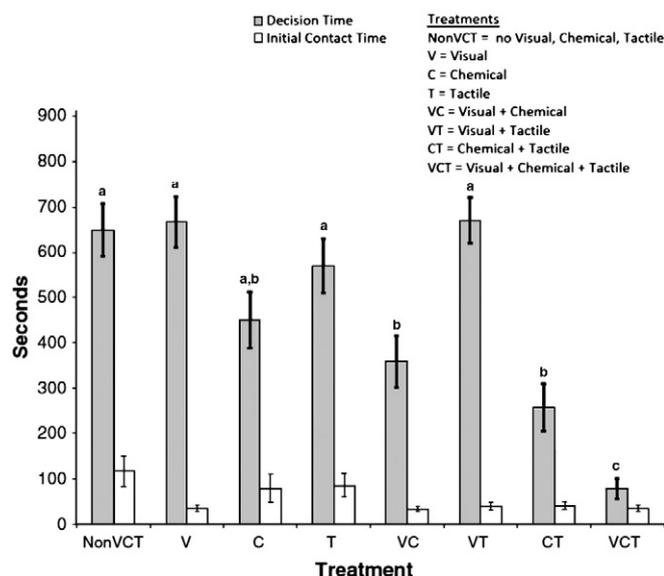

Fig. 4. The mean initial contact time and mean decision time during food acquisition treatments. Maximum time per session was 900 s. Treatments with the same letter represent those with no significant differences among them. Error bars represent ± 1.0 SE. Reduced decision times indicate faster food recognition. For comparison, the initial contact time for each treatment is indicated with unshaded bars. However, there were no significant differences among treatments (p > 0.05).
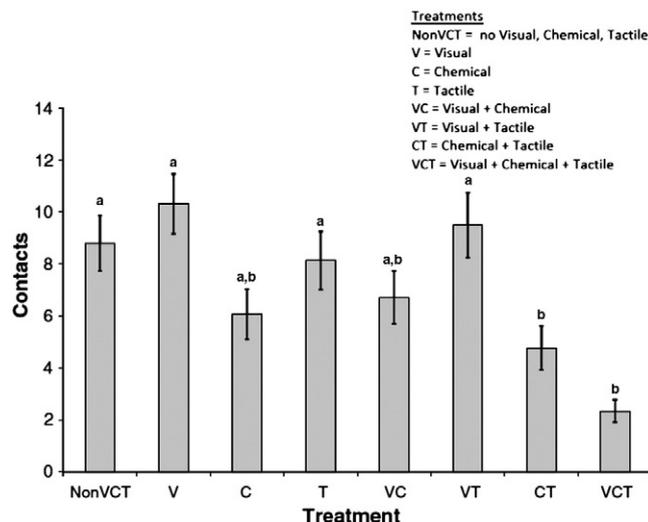

Fig. 5. The mean number of shell contacts during food acquisition treatments. Treatments with the same letter represent those with no significant differences among them. Error bars represent ± 1.0 SE. Reduced number of contacts indicates faster food recognition.

wax. In Fig. 4 it can be seen that the mean decision time was significantly different among treatments ($F_{7,245} = 35.06$, p < 0.001, partial $\eta^2 = 0.478$). Treatments that included the chemical cue (C, VC, CT, and VCT) had the lowest mean decision times, and there were no significant differences in decision times among these four treatments. Treatments without water-borne chemical cues (NonVCT, V, T, and VT) had the longest decision times, and there were no significant differences in decision times among these four treatments.

4. Discussion

4.1. Shell acquisition

In the hermit crab, *P. samuelis*, the ability to acquire a shell was significantly affected by which stimuli were presented. Tactile cues of shell availability had a stronger effect on shell acquisition behavior than visual or water-borne chemical cues.

Although one might expect that a specific stimulus, such as visual cues, might allow hermit crabs to locate shells faster than other stimuli, we found no significant difference among treatments in the time to initial contact with shells (see Fig. 2). Mesce (1993b) found that *P. samuelis* would find and inhabit a shell within 11 s under natural light, but required 190 s in the dark. In addition, she found that *P. samuelis* would "track" a black shell-shaped target as it was moved around the enclosure, showing a strong attraction to visual stimuli (Mesce, 1993b). However, in Mesce's study, the shell was the only object offered, while in our study four decoy objects were used in addition to the shell. Some species, such as the hermit crab, *Clibanarius vittatus*, can visually differentiate between gastropod species (Hazlett, 1982; Diaz et al., 1995). Reese (1963) noted that *P. samuelis* preferred shells that contrasted in color with the background, but could not visually differentiate between shell species. Other authors have observed that hermit crabs orient toward objects and shapes that represent shells (Reese, 1963; Diaz et al., 1995; Chiussi et al., 2001). Partridge (1980) found that *P. hirsutiusculus* preferred darkly colored shells when white and black painted *T. funebralis* shells were offered simultaneously. It is possible that that in our study, *P. samuelis* did not contact *T. funebralis* shells first because it was distracted by decoys.

In the current study, treatments that included the tactile cue of the natural, unwaxed shell elicited fewer contacts with the shell before a decision was made, than treatments that included a wax coated shell.

In all treatments that included the tactile cue (T, VT, CT, and VCT), the mean number of contacts approached one, indicating that hermit crabs recognized the shell on first contact. Because hermit crabs were tested without their shells, any shell that was encountered and recognized should have been readily inhabited. It is likely that *P. samuelis* is detecting calcium on the surface of the shell. Mesce (1982) found that both *P. hirsitusculus* and *P. samuelis* explored plaster replica shells longer if the replica contained calcium on its surface. In addition, both species were able to find and occupy buried shells every time when uncoated (calcium cue present), but were unable to find shells when coated with wax. Pechenik and Lewis (2000) also found that the hermit crab, *P. longicarpus*, relied on tactile cues to evaluate and select appropriate shells.

Treatments that included the tactile cue (T, VT, CT, and VCT) in our study, had significantly lower decision times than non-tactile treatments (NonVCT, C, V, and VC). Reese (1963) found that tactile cues had an over-riding effect on shell preference in *P. samuelis*, and tactile information cancelled out visual preference for dark colored shells. He also found that hermit crabs were able to select shells without visual and chemical cues following eye stalk and antennal ablation. In addition, *P. longicarpus* (Pechenik and Lewis, 2000) and *P. hirsutiusculus* (Mesce, 1993b), were shown to find shells in the dark as quickly as in the light, indicating that non-visual information, such as tactile cues, were used. In all likelihood, *P. samuelis* is utilizing chemoreceptors and proprioceptors located in the chelipeds while examining the surface cues of each object (Mesce, 1993a).

Alone, the water-borne chemical cue of gastropod odor or the visual cue of the shell was insufficient to significantly increase acceptance of the shell in the present study. In an experiment comparing the relative attractiveness of water-bourne chemical cues, Hazlett (1996b) found that a rocky intertidal hermit crab species was less influenced by odor than sandy or mud bottom species that had more reliable access to odor cues. It is likely that the unresponsiveness of *P. samuelis* to chemical cues of shell availability is also a result of living in rocky intertidal areas. However, in the present study, when chemical cues were combined with visual cues (VC) this combination significantly lowered mean decision time. While both Reese (1963) and Mesce (1993b) found that *P. samuelis* was visually attracted to *Tegula* shells, neither author tested the effect of adding chemical cues. Several other authors have noted that adding chemical cues of gastropod odor (Hazlett, 1982; Orihuela et al., 1992; Rittschof et al., 1995; Hazlett et al., 1996; Chiussi et al., 2001) or dead conspecific odor (Hazlett, 1996a; Rittschof and Hazlett, 1997; Gherardi and Atema, 2005), as signals of shell availability, increase hermit crab attraction to shells. In the current study, visual and chemical cues together could be used to acquire shells, but the time to insertion was significantly longer in the VC treatment compared to treatments with the tactile cue.

4.2. Food acquisition

In the context of foraging, *P. samuelis* was significantly affected by which stimuli were presented. There was a trend for water-borne chemical cues to have a stronger effect on feeding behavior than visual or tactile cues.

As in the shell acquisition experiment, the mean time to initial contact with the gastropod was not significantly different among treatments. It is possible that *P. samuelis* does not rely on visual cues for orientation toward food. Visual cues have been implicated in daily migration coordination, and are more likely to be important in hermit crabs that travel to foraging sites (Vannini and Cannicci, 1995) than for species, such as *P. samuelis*, that are opportunistic scavengers.

In treatments where the chemical cue was present (C, VC, CT, and VCT), hermit crabs made significantly fewer contacts with the gastropod and had significantly lower decision times, indicating that they recognized the gastropod as a potential food source faster than

during non-chemical treatments. When the gastropod aperture was sealed, hermit crabs explored the entire surface of the shell, and then usually released the shell and moved on to another object making no decision to feed. In most instances, once the hermit crab had discovered the open aperture and exposed foot muscle, feeding behavior initiated immediately. During the chemical treatment (C), the chemical cue was enough to override the lack of tactile cue, and hermit crabs investigated the wax coated shell until they found the aperture and decided to feed.

Chemical cues are implicated in a variety of hermit crab behaviors including: shell attraction (Hazlett, 1997; Chiussi et al., 2001; Gherardi and Atema, 2005); predator avoidance (Hazlett, 1996a; Rittschof and Hazlett, 1997); individual recognition (Gherardi and Tiedemann, 2004; Gherardi et al., 2005); and foraging (Hazlett, 1996a; Rittschof and Hazlett, 1997; Morton and Yuen, 2000). Because hermit crabs use chemical cues to locate the position of carrion and empty shells, they should be adapted to respond to the odor of their preferred gastropod species. Chemotaxi orientation would be of little value if the crab could not discriminate between the various odors present in seawater. In experiments conducted in the dark on the nocturnal rock crab, *Cancer irroratus*, the chemical stimuli of prey odors had a significant effect on foraging behavior, but the chemical cue of a competitive sympatric crab did not (Salierno et al., 2003). In their study, the presence of dead or injured mussel extract initiated foraging behavior immediately. In contrast, when the chemical signal was that of a live mussel, both chemical and tactile cues were necessary to initiate foraging.

In our study, for treatments that included the tactile cue of an uncoated shell, hermit crabs often engaged in "shell exploration" behavior, in which the shell was turned and the entire surface manually inspected. In non-tactile treatments with wax coated shells, hermit crabs would make contact with the shell, but discontinued further exploration. On ten occasions, hermit crabs removed the wax sealing the aperture and began feeding on the exposed *T. funebralis* muscle. This only occurred during Tactile and VT treatments, suggesting that tactile cues may have some effect on foraging motivation that was not specifically tested in this experiment. Although visually inspected, we did not test the water to determine if odor leakage had occurred. If leakage occurred, it could potentially explain why the T and VT treatments were not significantly different from the C treatment. There was no significant difference in decision time between groups C and CT, or between groups V and VT, suggesting that the tactile cue did not lower decision time and was therefore not a primary cue in making a feeding decision.

We found that in the shell acquisition experiment, the mean number of contacts with shells was lower in every treatment than the mean number of contacts with food in the food acquisition experiment (compare Figs. 2 and 4). In addition, the mean decision time was shorter in the shell acquisition context than in the food acquisition experiment in every treatment except groups C and T (compare Figs. 3 and 5). In another study, Billock and Dunbar (2009) suggested that being shell-less may be a greater motivating context than being hungry.

4.3. Contextual Decision Hierarchies

In the current study, hermit crabs utilized tactile (contact) cues over chemical (water-borne) and visual cues in their decisions to accept or reject shells. In contrast, when deciding to accept or reject food, hermit crabs utilized chemical over visual and tactile cues. Although similar information was presented in both situations, it was used differently by the hermit crabs in different contexts.

The results of this study support the idea that hermit crabs filter incoming visual, chemical, and tactile information such that a specific Contextual Decision Hierarchy of stimuli is utilized in decision-making. In the food acquisition experiment, we demonstrated that the

chemical cue was primary, eliciting the fewest contacts with the shell and the shortest decision times. In the shell acquisition experiment, the tactile stimulus elicited the fewest contacts with the shell and the shortest decision times. It may be that hermit crabs use visual information to locate shell-shaped objects, yet it is the tactile information that initiates the shell exploration and insertion behavior. When the shell was wax-covered, hermit crabs rarely initiated shell exploration behavior. In most instances however, once the hermit crab had discovered the shell aperture (even when the exterior was coated with wax) a decision was made within the immediate context, and the shell was quickly inhabited.

CDHs would benefit animals by providing rapid and accurate decision pathways when information is rich, and still allow for slower, yet appropriate decisions when information is limited. Shettleworth (2001) noted that for some animals, discrete stimuli compete for control of behavior such that one stimulus overshadows another in directing behavior, although the secondary stimulus alone can still elicit a response. Other research has shown that when sensory cues are presented either separately or in combination to animals, a sensory hierarchy is used to preferentially sort information (Stauffer and Semlitsch, 1993; Persons and Uetz, 1996).

The trigger to utilize a specific CDH may come from either the internal context (motivation) or the external context (environment). For example, male moths, *Spodoptera littoralis* will respond to the sound of a bat by freezing but will ignore the sound of a bat if female pheromones are detected (Skals et al., 2005), demonstrating that the moth's CDH changed from auditory to odor as the primary cue used in decision-making. Motivation, such as deprivation of food or shells, can focus hermit crab attention on the needed resource and initiate behavior (Billock and Dunbar, 2009). Elwood (1995) found that motivation significantly affects behavior in hermit crabs, such that crabs in suboptimal shells spend more time trying to access preferred shells, than crabs in optimal shells. In addition, the hermit crab, *P. longicarpus*, in inadequate shells responded to dead gastropod odor by increasing attraction to shells, but responded to dead conspecific odor, a signal of predator presence, by remaining motionless, thereby displaying the ability to make context-specific behavioral choices (Gherardi and Atema, 2005). It is possible that internal or external context triggers a release of hormones that alter the sensitivity of hermit crabs to specific cues since elevated hormone levels have been found in arthropods exhibiting specific behaviors (Fahrbach and Mesce, 2005; Briffa and Elwood, 2007).

While CDHs may be triggered by internal context, the external context may also influence specific CDHs. When the primary cue is absent or ambiguous, CDHs allow organisms to utilize secondary cues to complete the behavior. For example Chiussi and Diaz (2001) showed that in the fiddler crab, *U. cumulanta*, celestial cues (sun position) operate as the primary orientation cue, with beach slope and shore landscape operating as secondary cues. In the absence of celestial cues (cloudy days), slope or landscape could still be used to determine shoreward direction. When cues were ambiguous (i.e. when crabs were transplanted to a beach facing 180° opposite of the home beach) celestial cues overrode landscape cues. Thus, crabs oriented toward the sun's position correctly for their home beach, even though it was in opposition to landscape information at the transplantation beach. Chiussi and Diaz (2001) suggested that animals may be adapted to respond strongly to the most reliable cue, and less strongly to stimuli that are subject to random change. In our study, when tactile information was not available, hermit crabs could still use visual–chemical cues to acquire shells.

In the intertidal environment, resource availability information may be limited. In addition, hermit crabs may encounter a plethora of objects that are similar in characteristics to a shell, and could distract them from acquiring this needed resource. A hermit crab in an inadequate shell, or one that has lost its shell, must be able to locate an appropriate shell before it becomes injured or killed. By utilizing

multiple sensory cues, *P. samuelis* is able to evaluate the available information and decide to spend more or less time exploring an object, or to keep searching for a shell depending on both internal and external contexts. We suggest that Contextual Decision Hierarchies, therefore, allow *P. samuelis* to make the best possible decision from the information available at a specific time or location, and based on external and internal contexts. As the external context changes, CDHs allow animals to adjust their attention to alternate cues and still achieve their immediate goals.

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