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Evidence for "Contextual Decision Hierarchies"
In the Hermit Crab, *Pagurus samuelis*

by

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CHAPTER I

Introduction to Hermit Crab Behavior

In this dissertation I examine how sensory information is utilized by hermit crabs in decision-making. First, I confirm that hermit crabs deprived of resources, such as shells and food, are motivated to seek the needed resource at the expense of acquiring other potential resources from which they have not been deprived. Next, I explore the role of visual, chemical, and tactile cues in decision-making during three behaviors: shell acquisition; food acquisition; and predator avoidance. In light of the results from this research, I propose a new behavior model, 'Contextual Decision Hierarchies', in an effort to explain the differential use of sensory information in executing behaviors. In this chapter, I begin with a discussion of my research objectives and hypotheses that were tested. I then discuss the behavioral ecology of hermit crabs in general before commenting on *Pagurus samuelis* specifically. I then explore the sensory apparati that hermit crabs possess and comment on how sensory information is integrated to affect behavior.

Objectives

My have four main objectives for this dissertation: 1) to review the various behaviors and sensory processing associated with cognition in the context of crustacean biology; 2) to demonstrate that hermit crabs make behavioral choices based on motivation; 3) to determine if hermit crabs weight incoming information

into decision hierarchies during the execution of behaviors; and 4) to elucidate how decision hierarchies change based on context. These objectives were met through a review of the literature and a series of four experiments with the hermit crab, *Pagurus samuelis.*

In Chapter 2, I reviewed five attributes of cognition, and then reviewed behavioral experiments that demonstrated the underlying sensory processing of visual, chemical, and tactile sensory modalities that control and modify crustacean behavior. I concluded with a discussion of a new behavioral model.

In Chapter 3, I tested the hypothesis that hermit crabs deprived of food, shells, or both respond differently from control hermit crabs when presented with food and shells concurrently. This was measured by time to first contact with the needed resource, number of contacts, time to initiate behavior, and final behavioral choice. I found that for shell-less hermit crabs, the need to find a shell takes priority over obtaining food, while hermit crabs in adequate shells prefer not to risk switching shells even if one is encountered. When the risk of predation or exposure means imminent death, the motivation to seek shelter can outweigh the motivation to acquire food.

In Chapter 4, I investigated whether hermit crabs sort information about the environment, based on context, in order to make decisions quickly and efficiently. My first hypothesis was that visual, chemical, and tactile stimuli are arranged in a hierarchy such that one cue has a stronger influence on behavior than the other two. My second hypothesis was that the decision hierarchy varied by context, such that foraging and shell-seeking behaviors were directed by

different stimuli. These hypotheses were tested in food acquisition and shell

acquisition experiments. For each, I compared the time to first contact with the

resource (either food or shells), number of contacts with the resource, and

decision time, among treatments that included visual, chemical, and tactile cues

presented in a factorial manner. Results indicate that for the hermit crab, *P.*

samuelis, tactile information was primary in acquiring shells, but that chemical

cues were primary in obtaining food. I found that crabs were still able to locate

shells or food using secondary cues instead of the primary cue, although it took

significantly longer. I therefore propose that hermit crabs are utilizing "Contextual

Decision Hierarchies" to reduce information processing and make the best

possible decisions based on internal and external contexts.

In Chapter 5, I tested the hypothesis that shell acquisition behavior of the

hermit crab, *P. samuelis*, when removed from its shell and presented with various

predator cues varies, and that stimuli are arranged in a hierarchy of importance

in avoiding predators. Visual, chemical, and tactile cues were presented in a

factorial manner to determine if any sensory modality had a greater influence

than others. I found that hermit crabs utilize visual and tactile information to

detect predators, but use visual and chemical cues to acquire a shell in the

presence of a predator. Overall, visual cues may be most important to *P.*

samuelis in predator avoidance behaviors.

In Chapter 6, I concluded with an overview of my Contextual Decision

Hierarchy model and proposed areas for future research, after summarizing my

findings from Chapters 2 – 5.

Behavioral Ecology of Hermit Crabs

Most animals share the common needs of obtaining food, locating shelter, and avoiding predators. Sensory apparati are generally adapted to perceive information about the environment to meet those needs. However, the type of information most useful in completing one task may be very different from the type of information necessary to complete another. Perhaps animals focus on a key feature to scan for a resource or monitor for danger. For instance, an individual could utilize a visual search pattern when foraging, but monitor chemical information for predator odors. Narrowing the scope of simultaneous sensory processing would benefit any animal, but it is particularly important for invertebrate species that have limited neural processing capabilities.

From a hermit crab's perspective, resources such as food, shelter, and potential mates can all have the same outward appearance, that of a single gastropod shell species. Perhaps other sensory information, such as chemical or tactile cues, are utilized in conjunction with, or instead of, visual information in completing various tasks. Because many resources needed by hermit crabs for survival are ephemeral, especially in the intertidal zone, these animals must evaluate the relative worth of a resource upon detection. If they spend too little, or too much time evaluating a resource, they may be missing opportunities, or unduly wasting time and energy.

Unlike other decapod crustaceans that have fully hardened exoskeletons, hermit crabs have soft abdomens that make them more susceptible to predation and desiccation. This attribute requires them to protect their abdomens, usually

within empty gastropod shells, although other objects are sometimes used. Hermit crabs are found from deep ocean floors to terrestrial habitats, and from the poles to the tropics (Gage & Tyler, 1991; Brodie, 1998; Forest, *et al.*, 2000; Dunbar, 2001). Most intertidal areas have at least one hermit crab species in residence. Intertidal habitats are particularly vulnerable to changes in temperature and salinity and hermit crab species vary in their tolerance of these changes (Coffin, 1958; Dunbar & Coates, 2004). The use of gastropod shells has allowed hermit crabs to survive in a wide variety of environmental conditions.

Shells can be acquired from other hermit crabs, by locating empty shells, or by removing dead gastropods from their shells. Attraction to gastropod predation sites, a source of new shells, is mediated by both visual and chemical cues of injured gastropods (Hazlett, 1982; Rittschof, 1982). Occasionally hermit crabs will frequent sites known to contain available shells, such as octopus middens (Gilchrist, 2003) or hermit crab shell caches (Brodie, 1998; Greenaway, 2003).

Where hermit crabs are abundant, few unoccupied shells are usually found (Vance, 1972b; Elwood, *et al.*, 1979). Since the availability of shell species and shell sizes fluctuate seasonally, juvenile and adult hermit crabs may be affected disproportionately by shell availability causing distinct population bottlenecks at different life stages (Halpern, 2004). Studies have shown that often, hermit crabs occupy suboptimal shells in the field and will readily switch to a preferred shell size or shell species when provided (Reese, 1962; Vance, 1972a; Bertness, 1980; Rittschof, *et al.*, 1995; Floeter, *et al.*, 2000; Halpern,

2004; Tricarico & Gherardi, 2006). Shells are believed to be a limiting resource in most hermit crab populations.

Hermit crabs can be extremely selective in the species, size, and condition of shell they will accept (Elwood, *et al.*, 1979; Bertness, 1980). Preference can be based on shell size, shell weight, shell color, shell condition, internal volume, aperture size, or a combination of features (Reese, 1962; Reese, 1963; Partridge, 1980; Hahn, 1998; Floeter, *et al.*, 2000; Garcia & Mantelatto, 2001).

Shell selection and occupation consists of a complex series of behaviors. First, the hermit crab grasps the shell with its walking legs and runs the chelae over the surface of the shell (Reese, 1963; Mesce, 1982; Elwood & Neil, 1992). Next it rolls the shell over or crawls over the shell until it finds the aperture (Reese, 1963; Mesce, 1982). Once the aperture is found, chelae are inserted into the aperture and if found to be acceptable, the hermit crab will insert its abdomen into the shell (Reese, 1963; Mesce, 1982; Elwood & Neil, 1992).   The shell selection process involves multiple decision points, any of which can cause a hermit crab to reject a shell.

Shell adequacy has been shown to affect individual fitness. Vance (1972b) defined the 'Shell Adequacy Index' (SAI) as a ratio of predicted crab mass to actual crab mass in relation to shell size, such that SAI's less than 1.0 indicate shells that are too small and SAI's greater than 1.0 indicate shells that are too large for inhabiting hermit crabs. Occupying smaller-than-optimal shells (STO) reduces growth rate and increases the risk of injury and predation (Angel, 2000). Hermit crabs in STO shells may not be able to fully retract into their

shells, and are thus more susceptible to predation than those living in optimal shells (Vance, 1972a). Some studies have shown that egg clutch size can be limited by the size of shell the female occupies (Reese, 1969). STO shells reduce fitness and larger-than-optimal shells increase energetic costs. Hermit crabs should therefore be adapted to recognize and defend optimal shells.

In some situations, hermit crabs may choose shells that confer added advantages, despite being energetically expensive to inhabit. Hermit crabs that lived in high velocity water flow environments preferred heavier shells compared to hermit crabs that lived in still water habitats (Hahn, 1998). Yoshino, *et al.* (2004) found that during the mating season, males in large shells were more successful at mate-guarding than hermit crabs in small shells. Where durophagous predators are present, hermit crabs preferred more crush resistant shells (Bertness, 1981; Tirelli*, et al.*, 2000; Mima*, et al.*, 2003). However, there are costs to residing in heavy shells; hermit crabs that occupied heavier shells had elevated haemolymph lactate levels in comparison to those occupying lighter shells with the same internal volume (Briffa & Elwood, 2005). It is important for hermit crabs to obtain shells that offer the most benefits toward fitness and minimize the energetic costs of ownership.

Although shells offer some protection from predation, predators that have adaptations for feeding on gastropods are often able to use the same techniques against hermit crabs (Elwood & Neil, 1992). Some predators remove hermit crabs directly from shells, especially if the shells are too small for the crabs (Vance, 1972a; Angel, 2000; Tirelli*, et al.*, 2000). Predators that are known to

extract hermit crabs without breaking the shells include fish, octopods, crabs, and gastropods (Bertness, 1981; Tirelli, *et al.*, 2000; Gilchrist, 2003). Other predators break or crush shells to remove hermit crabs (Tirelli, *et al.*, 2000; Mima, *et al.*, 2003). *Pagurus longicarpus* will avoid shells containing holes drilled by gastropods presumably because these shells make them more vulnerable to predation (Pechenik & Lewis, 2000). Hermit crabs can utilize a variety of behaviors to avoid predation including: aggregation; falling off rocks to the cobble below; choosing thicker shells that are more crush resistant; withdrawing into their shells; and fleeing (Bertness, 1981; Hazlett, 1996a; Rittschof & Hazlett, 1997; Mima, *et al.*, 2003).

Hermit crabs are omnivorous and generally employ three modes of feeding; detrivory; filter feeding; and macrophagus scavenging (Elwood & Neil, 1992). As opportunistic scavengers, many species will eat large pieces of animal or plant detritus when encountered. Although hermit crabs will consume most types of carrion when available, choice studies have revealed they may prefer specific food types over others (Morton & Yuen, 2000). Thacker (1996) found the land hermit crab, *Coenobita compressus*, prefers to vary its diet between animal and plant material rather than consuming the first food type encountered when foraging. Wight, *et al.* (1990) conditioned the hermit crab, *Pagurus granosimanus*, to avoid a preferred food type. The ability to learn to avoid potentially harmful foods would be of great benefit to animals that consume a wide variety of detritus. Being able to take advantage of 'windfall' food

opportunities while maintaining a varied diet and avoiding potentially harmful foods should increase fitness.

Mating behavior is often complex in hermit crabs. Males can detect receptive females through chemical cues emitted by the females (Elwood & Neil, 1992; Yoshino, *et al.*, 2004). Hermit crabs must, at least partially, remove from their shells to copulate, as the ejaculatory ducts of the male are located within the coxae of the fifth pereiopods and the female openings of the oviducts are located on the third pereiopods (Elwood & Neil, 1992; Hess & Bauer, 2002). Females carry eggs attached to biramous abdominal appendages, called pleopods, until the eggs hatch (Elwood & Neil, 1992). Following hatching, larval crabs spend weeks to months going through developmental stages as plankton (Elwood & Neil, 1992). At the glaucothoe stage, young hermit crabs enter their first shell which they are able to find and inhabit without prior experience (Coffin, 1958; Reese, 1962). Sexual maturity may be reached in as little as four months and some reach maximum size within one to three years (Elwood & Neil, 1992).

Pagurus samuelis

Hermit crabs are crustaceans belonging to the order Decapoda and the infraorder Anomura. There are five families of hermit crabs: Coenobitidae, land hermit crabs; Diogenidae, left-handed hermit crabs; Paguridae, right-handed hermit crabs; Parapaguridae, deep-water hermit crabs; and Pylochelidae, non-gastropod shelter using hermit crabs (Martin & Davis, 2001). *Pagurus samuelis* belongs to the family Paguridae in which there are 32 genera and over 700

species of hermit crabs (Pechenik, 2005). The genus *Pagurus* contains 60

species (ITIS, 2008).

The blueband hermit crab, *Pagurus samuelis*, is a common upper-

intertidal zone resident found from British Columbia to Baja California (Reese,

1962; Abrams, 1987). Other sympatric hermit crab species, *P. granosimanus* and

P. hirsutiusculus, are usually found at lower intertidal zones (Abrams, 1987;

Hahn, 1998). In some locations, *P. hirsutiusculus* overlaps in tidal height with *P.*

samuelis (Abrams, 1987; Mesce, 1993a), although *P. samuelis* prefers rocky

intertidal areas and *P. hirsutiusculus* prefers sandy bottom tide pools (Reese,

1962). As an inhabitant of the upper intertidal zone, *P. samuelis* can tolerate

fluctuations in temperature, pH, and salinity (Coffin, 1958; Reese, 1963). In

laboratory experiments, *P. samuelis* was capable of evicting more *P.*

hirsutiusculus from shells than the other way around and *P. samuelis* occupies

empty shells more rapidly than *P. hirsutiusculus* (Abrams, 1987). It is unclear if

P. samuelis and *P. hirsutiusculus* do not generally live in the same tide pools due

to physical tolerance differences or interspecific competition (Reese, 1969;

Abrams, 1987).

Following mating, *P. samuelis* releases larvae in the spring and summer

(Abrams, 1987). The four zoea stages typically require 22 days at 17° C and the

glaucothoe stage takes 10 days. The total time for juvenile molts averages 38

days and maturity is reached around 70 days (Coffin, 1958).

Mature *P. samuelis* prefer shells of the black turban snail, *Tegula*

funebralis (Reese, 1962; Abrams, 1987; Mesce, 1993a; Hahn, 1998). The thorax

and abdomen of *P. samuelis* are narrow and circumferentially round with little tapering towards the posterior, bearing a striking resemblance to the internal shape of *Tegula* shells (Mesce, 1993a). They will readily switch shells in laboratory choice experiments (Abrams, 1987).

Hermit Crab Sensory Apparati

As with most crustaceans, hermit crabs possess stalked compound eyes with thousands of ommatidia (Pechenik, 2005). Hermit crabs are attracted to specific shapes that correspond to shells or habitat features and will withdraw from shapes associated with predator features (Orihuela*, et al.*, 1992; Diaz*, et al.*, 1995; Chiussi*, et al.*, 2001). Behavioral evidence suggests that hermit crabs can visually discriminate between shell species (Hazlett, 1982; Diaz*, et al.*, 1995). Some hermit crabs prefer specific colors of shells, either due to visual contrast, which makes the shell easier to find, or visual camouflage that makes the shell more cryptic when occupied (Reese, 1963; Schone, 1964; Partridge, 1980). Hazlett (1996b) concluded that hermit crabs visually determine which hermit crabs to exchange shells with based on the opponents' inability to withdraw into shells. It is unclear what role vision plays in the shell-seeking behavior of *P. samuelis*. Mesce (1993a) found that *P. samuelis* relied on visual cues for locating shells, but Reese (1963) concluded that visual information was not necessary.

The effect of chemical cues can be determined by testing the behavioral response of hermit crabs in the presence of various odors. Decapod

crustaceans have millions of chemosensory neurons. In addition to having pairs

of both antennae and antennules, hermit crabs have multiple organs of

chemoreception, including antennal sensilla, antennular aesthetascs, and

cheliped setae and sensilla (Mesce, 1993b). Aesthetasc sensilla, found only on

the distal half of antennular flagella, are chemosensory (Derby & Steullet, 2001).

Sensilla are receptor neurons packaged into cuticular extensions.

Chemosensory structures vary in sensitivity not only in the chemical compounds

detected, but also the distance at which chemical odors can be detected.

Because hermit crabs use chemical cues to locate the position of carrion

and empty shells, they are adapted to respond to the odor of their preferred

gastropod species (Hazlett, 1982; Mesce, 1993b). Chemotaxi orientation is

accomplished by discriminating between various odors, concentrations, and

directional flow in seawater. Hazlett (1982) tested *Clibanarius vittatus* for its

attraction to two species of gastropod shells in the presence of odor from each

shell. Crabs oriented to the corresponding shell when that species' chemical

odor was presented in the aquarium. Gherardi and Atema (2005) demonstrated

that *Pagurus longicarpus* responded to dead gastropod odor by increasing

locomotion in search of an available shell but responded to dead conspecific

odor by remaining motionless as an anti-predator response. Hermit crab

dominance hierarchies and individual recognition may also be a function of odor

recognition (Gherardi & Tiedemann, 2004; Gherardi, *et al.*, 2005). Hermit crabs

are sensitive to a wide variety of chemical cues and these cues affect behavior.

Processing of tactile cues includes both chemo-reception while in contact with an object and pressure sensitivity used in texture differentiation. Some sensilla are chemo-mechanosensory, including: hair pegs; hedgehog sensilla; fringed sensilla; hooded sensilla; and simple sensilla (Derby & Steullet, 2001). Bi-model sensilla (chemo-mechano) are useful for identifying the spatial location of chemo-tactile stimuli (Derby & Steullet, 2001).

While detection of amino acids, hormones, and proteins can occur at a distance, calcium detection occurs through the physical contact of chela sensilla with the substrate (Mesce, 1993b). The ability to detect if a specific object contains calcium would aid hermit crabs in differentiating shells from pebbles whether visible or not. *Pagurus samuelis* explored plaster replica shells longer if the shell contained calcium on its surface, and was able to find and occupy buried shells every time when uncoated (calcium cue present), but never found them when shells were coated (Mesce, 1993a).

Tactile information such as texture and pressure are used by hermit crabs in conspecific interactions and resource location. Hermit crabs use shell "rapping" as a clearly defined agonistic signal to acquire a shell that is occupied by another hermit crab (Briffa & Elwood, 2002). Attackers that rapped with high intensity and temporal repetition in the first four bouts were more successful than those who rapped at a low intensity (Briffa & Elwood, 2002), indicating that hermit crabs evaluate their opponent's strength through tactile cues. Females use male cheliped "tapping", an additional use of tactile communication, to signal readiness to mate (Hazlett & Rittschof, 2000). In an experiment with three sympatric

Clibanarius species, Turra and Denadai (2002) found that all three showed substrate texture preferences. Tactile information is utilized for locating shells, conspecific communication, and habitat selection.

Decision-Making and Cognition

Behavioral experiments have begun to investigate how hermit crabs integrate information to make behavioral choices. For instance, prior experience with frequency of encounter rates can be used as a decision criterion by hermit crabs. Wada *et al.* (1999) found that during the annual mating of *P. middendorffii,* males guarded females earlier when female encounter rate was low (once per day), than when encounter rate was high (four times per day), even when the male to female ratio was kept constant. Guarding duration was longer when the sex ratio was male biased. This species appears to be able to keep track of encounter rate and use that information to make decisions that will maximize its chances of reproducing during the annual mating season. Mesce (1993a) demonstrated that *P. samuelis* is able to spend less time exploring, and in effect "ignore" shells that it has already rejected for occupation. Other species of hermit crabs have shown the ability to remember which shells they have encountered (Jackson & Elwood, 1989; Hazlett, 1995). Evaluating conspecific encounter rates and remembering previously encountered shells requires the storage of information in short-term memory.

Several hermit crab species are known to exhibit homing behavior which requires a level of spatial cognition. *Coenobita clypeatus* not only returns to a

very specific location, but it also stores empty shells in a cache for future (Brodie, 1998). *Pagurus longicarpus* utilizes both celestial cues (Rebach, 1978) and substrate slope (Rebach, 1981) to complete annual migrations to deeper water. *Clibanarius laevimanus* is able to return to its home mangrove tree after daily foraging or experimental displacement up to 5 m away. It appears that multiple cues are used in hermit crab homing behavior. Rebach (1981) notes that there is evidence that orientation cues are arranged hierarchically, and that hermit crabs may shift to a secondary cue when the primary cue is not available.

Although hermit crabs may possess the ability to detect visual, chemical, and tactile cues, their neural processing capabilities may restrict the amount of information that can be simultaneously utilized for decision-making. This would necessitate the use of a primary cue in directing specific behaviors. However, at times, the primary cue may be unavailable or ambiguous, so it would benefit an animal to be able to switch to other stimuli in decision-making. Efficient decisions could therefore be made by focusing on a primary cue during a context, while using secondary cues only when needed to reinforce or replace the primary cue.

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CHAPTER II

Contextual Decision Hierarchies in Crustaceans

Abstract

In this review of crustacean cognition, I discuss five attributes of cognition: attention; representation; learning; solving novel problems; and contextual modulation. Behavioral experiments have demonstrated the underlying sensory processing of visual, chemical, and tactile information that controls and modifies crustacean behavior. I propose that information is prioritized into hierarchies for efficient processing. I define "Sequential Decision Hierarchies" (SDHs) as the use of specific sensory cues in the execution of a series of discrete steps in a behavior. During the use of SDHs, one stimulus initiates the first behavior, another cue initiates the second behavior, and so on until the task is completed. I contrast SDHs with the novel concept of "Contextual Decision Hierarchies" (CDHs), which occur when various sensory modalities are ranked in order of influence on a single behavior. CDHs enable animals to direct their attention to a single sensory modality during a behavior, yet maintain the flexibility to switch to a secondary or tertiary stimulus if the primary one is unavailable or ambiguous.

Introduction

While the environment is full of potential information, species, and even individuals within a species, vary in their ability to detect, evaluate, and act upon this information. Those animals that can perceive, process, and interpret the most reliable cues available in their habitat have an adaptive advantage over individuals with less refined cognitive abilities.

Cognition Definition

Animal behavior is sometimes divided into the "noncognitive", or reflexive, and the "cognitive", or flexible behavior. In the broadest sense, cognition can be defined as the acquisition and processing of information by animals (Dukas, 1998b). "Cognition, broadly defined, includes perception, learning, memory and decision making, in short all ways in which animals take in information about the world through the senses, process, retain and decide to act on it" (Shettleworth, 2001:277). Cognition involves processes that operate on the relations between environment and behavior (Timberlake, 2002). Cognition can also be defined as the ability to step out of the bounds of the innate and perform mental operations or make decisions (Gould, 2002).

Since cognition underlies behavior (Dukas, 1998b), cognition plays a significant role in evolutionary change. For cognition to evolve, natural variation in individual ability must exist within the population and the differences must have adaptive consequences (Burghardt, 2002). The evolution of cognitive abilities can be considered a subset of the evolution of plasticity in behavior. Behavioral adaptation plays a central role in evolution. Edward O. Wilson (1975:13) and

Ernst Mayr (1982:612) both call behavior "the pacemaker" of evolutionary change. Recently the role of specific genes in behavior, learning, exploration, and motivation, has been studied by eliminating specific genes in inbred animals (Burghardt, 2002).

Research design is difficult to formulate in such a way as to designate clear behavioral criteria for processes in animals. The most that one can say is that this animal "behaves as if it knows" a particular mental computation. Timberlake (2002) suggested an approach to animal cognition based on constructing the mechanisms, function, and evolution of cognition in one species at a time.

Cognitive Processes

Dukas and Real (1993) listed six cognitive stages: reception (receiving sensory information about the environment), attention (focusing on a subset of potential information), representation (maintaining a mental image), memory (retaining information), problem solving (deriving pathways to achieve goals), and communication language (influencing others by manipulating symbols). Some examples of behavior that imply cognition are: intentional deception; episodic-like memory; and using a social or physical concept to solve a specific novel problem (Shettleworth, 2001). Gould (2002) included the cognition criteria of planning novel responses and forming concepts. He defined "concepts" as learned abstractions independent of the exemplar. For example, an animal may remember a specific pattern or odor and associate that with the concept "food".

The purpose of this manuscript is to discuss biology the various behaviors and the sensory processing associated with cognition in the context of crustacean, and to suggest a new direction for future cognition research. I will discuss five attributes of cognition based on the definitions of several authors.

     1. Attention (Dukas & Real, 1993)

     2. Representation (Dukas & Real, 1993; Gould, 2002; Saidel, 2002)

     3. Learning (Dukas & Real, 1993)

     4. Solving novel problems (Dukas & Real, 1993; Shettleworth, 2001)

     5. Contextual modulation (Shettleworth, 2001)

Next, I will discuss how visual, chemical, and tactile sensory modalities operate to control and modify crustacean behaviors that indicate cognitive processing. In addition, I propose a new behavioral model; "Contextual Decision Hierarchies," which may lead to further understanding in the field of animal cognition. Although examples will come primarily from crustacean research, studies involving other invertebrates as well as vertebrates provide important insights into cognitive processes. I conclude with a discussion of the impact of environmental disturbance on animals and their cognitive processes.

Attributes of Cognition

In this section I will expand on the five aforementioned attributes of cognition. For each attribute, I will briefly define the attribute, provide exemplars for various taxa to clarify, and review the published evidence that crustaceans possess that attribute.

Attention

An important function of the cognitive system is to initially reduce the amount of information to be processed while emphasizing the information that is most relevant to fitness (Dukas, 1998b). Attention can be described as the narrow mental focusing on a specific subset of all available information perceived by an organism. Selective attention allows an animal to filter out irrelevant information and direct its attention to a specific pattern or cue useful for decision-making (Dukas, 1998a).

For example, during homing and foraging behaviors, an animal must stay focused on the goal both during the outward and homeward journeys, and even adjust for errors during locomotion. Homing pigeons rely primarily on celestial cues for orientation; however, olfactory, magnetic, and low-frequency sound cues have also been shown to contribute to pigeon orientation (Hagstrum, 2000). Jumping spiders of the genus *Portia* stalk and prey on other spider species. Jumping spiders can display remarkable attention in stalking a single spider amongst many possible nearby spiders and remaining focused on one prey item through all of the various predation techniques in their repertoire (Wilcox & Jackson, 2002).

Bees have also been shown to focus on a primary cue during orientation. The walking honeybee, *Megachile rotundata*, utilized nest edge distances to locate the opening of the hive (Fauria*, et al*., 2004). The honey bee, *Apis mellifera*, focused on sun compass direction rather than landmark cues when returning to the nest, perhaps due to poor visual discrimination of landmarks

(Menzel, *et al.*, 1998). In another study, Chittka, *et al.* (1995) found that *A. mellifera* responded to trained flight distances more strongly than visual landmarks when flying to feeding sites. I suggest that relying on a single cue serves not only to reduce the mental processing load, but also to reduce possible error from low acuity sensory modalities that in some situations may be misleading.

Vannini & Cannicci (1995) offered a review of homing behaviors seen in crustaceans. The spider crab, *Inachus phalangium*, used visual rather than chemical cues to locate reproductive females on sea anemones. The crab, *Eriphia smithi,* used visual cues of its home cliff to nocturnally forage and return home but became disoriented when blinded or taken to a dissimilar novel cliff. The swimming crab, *Thalamita crenata,* could visually orient toward home when placed up to 20 m away, but not when placed 50 m from their home. Some crustaceans, such as the mangrove crab, *Sesarma leptosoma*, and the hermit crab, *Clibanarius laevimanus*, exhibit daily migrations to feeding grounds, yet return to a specific home tree after foraging.   Brodie (1998) individually marked the terrestrial hermit crab, *Coenobita clypeatus,* and tracked them on a small island of Honduras. The hermit crabs returned to very specific locations, suggesting that they possess well-developed homing abilities and specific home ranges, and may even carry empty snail shells to hidden shell caches presumably for future use. Although the sensory modalities utilized in homing behavior are not always known, the ability to return to a specific location demonstrates focused attention on a goal.

Crustaceans can also focus attention on a specific predator cue or shelter cue to avoid predation. When presented with various 'dummy' predator objects, the mangrove climbing crab, *S. leptosoma*, reacted most strongly to dummy crabs that possessed an open claw, indicating that claws were the cue that alerted them to danger (Cannicci*, et al.*, 2002). Megalopae of the blue crab, *Callinectes sapidus*, reacted to solid objects (corresponding to predators) by swimming away and reacted to vertical stripes (corresponding to seagrass) by swimming in all directions (Diaz*, et al.*, 1999). When predator odor was presented, juvenile mangrove crabs, *Aratus pisonii*, were strongly attracted to black, vertical rectangles, possibly as a cue of mangrove roots (Chiussi, 2002). The hermit crab, *Clibanarius antillensis*, retreated from solid objects when removed from its shell and presented with predator odor (Chiussi*, et al.*, 2001). Focusing attention on a single cue or attribute likely improves the reaction time of prey animals.

Crustaceans can also focus attention on a specific attribute when acquiring resources. For example, chemical cues are often implicated in the foraging behavior of crustaceans, such as: the spiny lobster, *Panulirus argus* (Derby*, et al.*, 2001); the California spiny lobster, *P. interruptus* (Zimmer-Faust & Case, 1983); the rock crab, *Cancer irroratus* (Salierno*, et al.*, 2003); the crayfish, *Orconectes rusticus* and *Procambarus clarkia* (Moore & Grills, 1999; Steele*, et al.*, 1999); and the hermit crab, *Clibanarius vittatus* (Hazlett, 1996a; Rittschof & Hazlett, 1997). For hermit crabs seeking shells, individual chemical, visual, and tactile cues have all been implicated in shell selection behavior. Both *C. vittatus*

(Hazlett, 1996b) and *Pagurus samuelis* (Reese, 1963) can locate appropriate

shells using visual cues. In the absence of chemical and visual cues, tactile cues

alone can be used to acquire shells (Mesce, 1982; Pechenik & Lewis, 2000;

Billock & Dunbar, submitted-b).

Crustaceans display the ability to focus on a specific goal or concept

during the execution of a task and the ability to focus on a single sensory cue to

facilitate effective and timely behavior completion.

Representation

All animals seem to possess at least some "working memory", or short-

term information storage (Dukas, 1998b). For this to occur, neurons that process

incoming information must be able to retain a representation of the information,

at least for a short period. Arthropods often use shortcuts of identifiable features,

such as color, movement, or position in the visual field, to quickly recognize

resources, mates, and predators (Collett*, et al.*, 1997).

Saidel (2002) asked whether animals respond to the world directly, or if

they make mental representations of the world and respond to those

representations. For instance, does an ant remove a dead conspecific from the

colony because it recognizes that the ant is "dead" or is it merely responding to

the odor of a decaying body that must be removed? One possible line of

evidence is an animal's ability to find alternate routes to a goal when the

preferred route is blocked. This requires that the animal relinquish its preliminary

plan of achieving the goal and maintain a mental focus on the goal while

conceiving of an alternate solution. It would seem that some animals are not

merely responding to their world directly, but are instead, making pictorial, or language-like, representations of the world so that mental processing of the information can occur.

Even the simplest spatial orientation involves detection and recognition of a goal as well as the association between sensation and movement to reach the goal. Orientation toward reliable resources within a habitat may require learning and remembering otherwise neutral cues (Shettleworth, 2002). Different cues demand different mental computations. For example smells, sights, and sounds may emanate from a location and serve as a beacon, while internal cues generated by the animal's own movement may allow it to keep track of where it is relative to a known starting point, and use this information in "dead reckoning" orientation (Shettleworth, 2002).

In higher order vertebrates, communication behavior demonstrates the use of mental representations. For example, adult vervet monkeys employ a variety of predator alarm calls: they will look up and take cover when an avian alarm call is given; climb into trees when the leopard call is given; and check out the grass in response to a snake alarm call (Strier, 2003:300). In fact, when a group of Japanese macaques was transferred to a ranch in southern Texas, they developed a new alarm call to signify rattlesnakes, a novel predator (Strier, 2003:301). Primate use of symbolic communication implies that they are using mental representations of predators and can communicate that representation to others.

Three lines of evidence point to the use of representations by invertebrates: predator-type recognition; social recognition; and resource value recognition. Predator-type recognition is possible when animals vary anti-predator tactics in response to recognition of different predators. The marine snail, *Planixis sulcatus*, appeared to recognize different types of predators; hiding in crevices in response to shell crushing predator cues, and emerging out of the water in response to predatory snail cues (McKillup & McKillup, 1993). The hermit crab, *Pagurus filholi*, responded to shell-crushing crab odor by fleeing, but responded to dead conspecific odor by remaining motionless (Mima*, et al.*, 2003). In cases where the predator is unknown, a general immobilization tactic may be most effective. The hermit crab, *Diogenes pugilator*, responds to sea stars by burying in the sand, to octopi by withdrawing into its shell, and to crabs by fleeing (Tirelli*, et al.*, 2000). The hermit crabs, *Calcinus obscurus* and *Clibanarius albidigitus*, withdrew into shells in response to crab predators, but dropped off rocks into crevices below when predatory fish swam by them (Bertness, 1982).

Social recognition is the ability of individuals to recognize each other on the basis of one or more identifying cues, and to make an association to past experiences with that individual. The cleaner shrimp, *Lysmata debelius*, recognized its mate even after six days of separation (Rufino & Jones, 2001). The hermit crab, *Pagurus longicarpus*, distinguished between familiar and unknown conspecifics and exhibited dominance hierarchies (Gherardi & Tiedemann, 2004). Gherardi*, et al.* (2005) went on to further demonstrate that

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individual recognition was based on individual odor cues. The association between recognition cues and past experience allows mating pairs and dominance hierarchies to form. This requires a type of mental representation in invertebrates, such that animals have a "concept" of other individuals and possibly high-order knowledge about conspecifics.

Resource value recognition can be seen in hermit crab shell fighting behavior. Shell fights among hermit crabs offer opportunities to study the value an individual places on a resource, since the shell itself can have an "objective value" based on its condition as well as a "subjective value" to a particular hermit crab based on the individual's current need. The hermit crab, *Pagurus longicarpus*, in smaller-than optimal (STO) shells was more motivated and fought longer than crabs of the same size and rank in optimal shells (Gherardi, 2006). In addition, Hazlett (1996b) concluded that the hermit crab, *C. vittatus*, evaluated it's opponent's likelihood to switch shells when deciding which hermit crabs to engage in a shell fight. The opponent's shell fit, and by extension, its motivation to switch shells, could be calculated by the initiator because a hermit crab that can not fully retreat into its shell is in a shell too small, and a crab that retreats too far into the shell is in a shell too large.

Although the nature of actual memory and mental representations that individuals are capable of remains a mystery, I propose that predator, social, and resource recognition evidence support the concept that some invertebrates possess this ability.

Learning

Although most information from working memory soon vanishes, some relevant information becomes stored in long-term memory (Dukas & Real, 1993). In a sense, some information is pre-processed so that animals can act upon the information quickly when perceived. The ability to learn from prior experience may be adaptive if it allows individuals to process information faster and more accurately than if the situation is novel at each encounter.

Research with vertebrates has demonstrated not only that individuals vary in their ability to learn, but also that learned behaviors are heritable. Shettleworth (2002) observed that chickadees, which store food, had better spatial memory and could learn food locations better than juncos, which do not store food, even though both species remember color and location. Work by Burghardt (2002) showed how the behavior, temperament, and personality of individual neonatal garter snakes differ at birth and appear to be heritable. Snakes that learned to switch from their natural diet of earthworms to mosquito fish passed the learned preference for fish on to their offspring; and those who learned, grew better on fish than on worms.

Invertebrates have also demonstrated a remarkable ability to learn behaviors that improve survivability. The grasshopper, *Schistocerca americana,* reared with access to a food source that was consistent in spatial location, color, taste, and nutritional value experienced a higher growth rate than those reared with food sources in which those attributes vary (Dukas & Bernays, 2000). Learning the cues that indicate appropriate foods can decrease the time spent

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foraging, time spent exposed to predators, time between meals, and time spent digesting nutritionally deficient food.

Bees have long been studied for their remarkable abilities to remember flower preferences, flower handling techniques, location of their hive, and foraging routes; both those experienced and those communicated through other bees. Chittka and Thomson (1997) found that bees could remember two different maze pathways and associate the correct path with the color of the artificial "flower" they entered. Preliminary tests by Gould (2002) have shown that honey bees can learn to recognize specific odors, colors, shapes, and even English letters independently of size, color, position, or font. In normal learning, there is incremental improvement beginning with the first test; however, in some tasks it required 30 to 40 training sessions before honey bees responded correctly, leading Gould (2002) to surmise that bees were experiencing "concept learning."

Various experiments have shown that crustaceans can utilize the memory of recent experiences to change their response to specific cues, as evidenced by conditioning studies. The crab, *Chasmagnathus granulatus*, has been conditioned to avoid the light (Denti*, et al.*, 1968) and the crab, *Carcinus maenas*, conditioned to press a lever to receive food (Abramson & Feinman, 1990). Spiny lobsters have been conditioned to avoid naturally attractive chemicals and to increase attraction to other food related chemicals (Derby*, et al.*, 2001). The hermit crab, *Pagurus granosimanus*, was conditioned by Wight*, et al.* (1990) to reject an attractive but novel food when severe illness was induced by injecting

lithium chloride following initial ingestion of beef. Hermit crabs learned to avoid

beef after only 1-2 trials while continuing to feed on fish, indicating that this was

learned aversion and not just a cessation from all feeding. Since many hermit

crabs are detritivores, learned food aversion would enable them to subsequently

avoid a wide variety of toxins they undoubtedly encounter (Wight, *et al.*, 1990).

A key element in learning capability is storing information about the

environment or events in memory. Jackson & Elwood (1989) demonstrated that

the hermit crab, *Pagurus bernhardus*, investigates novel shells longer than

familiar shells, thus indicating an ability to remember individual shells. Mesce

(1993a) had similar results with *P. samuelis*, which ignored familiar shells that

were previously rejected. The land hermit crab, *Coenobita compressus*, prefers

to eat a food item different from the one last consumed, requiring at least a

temporary memory of what the last food item was (Thacker, 1996). Toncoso &

Maldonado (2002) have shown that *Chasmagnathus* crabs possess two forms of

long-term memory, one associated with the environment, "context signal

memory", and one associated only with the stimulus, "signal memory". Both the

behavior patterns and neural receptors differ between these memory types.

Learning benefits organisms by improving functioning with experience and

reducing the decision time of subsequent encounters with familiar situations.

Problem Solving

The cognitive ability to solve problems can range from the relatively

simple, such as avoiding detection by a predator while foraging, to the overtly

complex, such as the use of tools. Primates are a well known example of

possessing tool-related behaviors such as threat displays, constructing shelter, and acquiring food (Strier, 2003). While vertebrate problem solving capabilities may be taken for granted, it is the range of invertebrate problem solving capabilities that deserves mention. Both social and solitary invertebrates are capable of sophisticated problem solving.

Social invertebrates such as ants, bees, and wasps can utilize division of labor to achieve goals that individuals can not accomplish alone. Other invertebrates are also capable of solving problems in groups. The social spider, *Stegodyphus dumicola*, forms foraging societies to hunt cooperatively and digest large prey items by group member injection of enzymes (Whitehouse & Lubin, 1999).

Wilcox & Jackson (2002) reviewed a wide variety of predation techniques jumping spiders employed. The jumping spider, *Portia*, was highly efficient in capturing spiders and was even adept at capturing novel spider species upon first exposure in the laboratory. Some *Portia* species were able to recognize spider species and adjust their predatory style accordingly. For example, laboratory reared Philippine *Portia* innately knew to approach a spitting spider from the rear. Jumping spiders mimicked a struggling insect and continued to vary the intensity and pattern of the web strumming until the prey spider responded. *Portia* used the camouflage of a gentle breeze to mask its own movements while approaching the prey. If the stealth movements of *Portia* were detected, it would scramble off of the web, climb around the surroundings, and drop in from above to capture the unsuspecting spider. The jumping spider also

exhibited the ability to utilize detours that sometimes take it out of visual contact with its prey spider.

A variety of conditioning experiments have shown that crustaceans possess the behavioral flexibility to solve novel problems, such as: feeding in a specific location; feeding in the presence of a color cue; navigating a maze; finding water in a cup to moisten gills; or detaching food from a hook suspended above the animal (Schone, 1964). It is quite possible that crustaceans exhibit a wide variety of problem solving behaviors that have hitherto not been experimentally investigated.

Contextual modulation

Behaviors may be mediated by a representation of the information and modulated by the context of the information (Shettleworth, 2001). Contextual modulation allows animals to make appropriate decisions based upon the current situation. Informed decisions assume at least a minimal evaluation of potential risks and rewards. Recent studies have shown the importance of contextual modulation in structuring animal behavior. For example, rats can learn that when a light is on, bar pressing releases chow but when a tone is on, chain-pulling releases chow (Shettleworth, 2001). Another example is the "audience effect" in which an animal will give an alarm call more in the presence of other animals than when alone (Shettleworth, 2001).

Within the arthropods, bees have demonstrated remarkable use of context information to adjust behavior appropriately in completing tasks. Collett, *et al.* (1997) suggested that bees use "contextual priming" of memories to organize

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knowledge and retrieve memories. They trained bees to recognize one pattern at site A and a different pattern at site B, 40 m away, demonstrating that the location context of landmarks primed bees to pick the correct object at each site. Collett and Kelber (1988) trained bees to enter two huts and collect a sucrose drop at blue cylinders in one hut, but from yellow cylinders in the other hut. Lotto and Chittka (2005) trained bumblebees to forage from yellow artificial flowers under green light (simulating understory illumination) and to forage from blue flowers under blue light (simulating open field conditions). In another experiment, bees were trained to go to yellow flowers in dim light, and to blue flowers in bright, white light (Lotto & Chittka, 2005). Bumblebees are able to use the contexts of color or illumination level to correctly choose flowers, potentially as a signal of location or habitat type. Bees have also learned to associate specific flowers with the processing techniques necessary to acquire the pollen or nectar from that species (Chittka & Thomson, 1997) and to associate time of day with a specific color of flower at which to feed (Gould, 1987). For bees, the ability to associate location, flower shape and color, illumination level, and even time of day with feeding behaviors has enabled them to take advantage of contextual cues that improve foraging success.

Crustaceans have also demonstrated the capacity to adjust their behavior in response to specific contexts. For example, foraging animals will modulate anti-predator behavior in response to perceived risk level. Hemmi (2005b) found that the fiddler crab, *Uca vomeris*, responded to predator approaches with increasing speed of escape as distance from its shelter increased. Hermit crabs,

such as *C. vittatus* and *P. filholi*, responded to added predator odor by increasing

locomotion (Hazlett, 1996a; Mima*, et al.*, 2003). Hermit crabs also discontinued

shell acquisition, food acquisition, and mating activities, when predator odor was

added (Hazlett, 1997; Rittschof & Hazlett, 1997; Hazlett & Rittschof, 2000). This

indicates that when the context changes, such as the arrival of a predator,

crustaceans can appropriately alter behaviors.

Mating decisions are also modulated by context and perceived likelihood

of success. Male American lobsters, *Homarus americanus*, based sperm

allocation on the relative size of females and matched the amount of ejaculate to

the size of the female (Goselin*, et al.*, 2003). The fiddler crab, *Uca annulipes*,

has a six day mating cycle and females tended to be more choosy during the

early days of the cycle, with their acceptance threshold lowering as the cycle

proceeded (Backwell & Passmore, 1996). Wada *et al*. (1999) showed that for the

hermit crab, *P. middendorffii*, which only spawns once per year, males determine

when to begin mate-guarding by evaluating female encounter rate. During

mating behaviors, both males and females can alter reproductive strategies to

improve success rate in light of the current context. Accurate behavioral

decisions require at least some evaluation of the current conditions as well as the

internal state of the animal.

Crustacean Sensory Processing

Reception, the intake of external information through any of the sensory

modalities, is the first stage of cognition according to Dukas and Real (1993).

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Documenting the behavioral choices made in response to specific cues has shed light on the relative influence of various cues on cognitive processes. When studying animal responses to stimuli, consideration should be given to the species-specific sensory organs and neurological processing that intervenes between the signal and its behavioral effect (Shettleworth, 2001). Although the relative influence of specific stimuli on behavior has been studied in a variety of taxa, this section of the review will specifically focus on crustacean sensory processing.

Visual

Most crustaceans possess compound eyes with visual capabilities ranging from simple light detection to complex color, ultraviolet, and polarized light vision. Of animals that have been tested, photoreceptors of most crustaceans are tuned to red wavelengths. However, blue absorption has been found in some barnacles and crayfish (Shaw & Stowe, 1982). Spectral sensitivity varies between deep-sea organisms that experience short wavelength blue light, and near-shore organisms that are exposed to longer wavelength yellow light (Johnson, *et al.*, 2002).

Zeil and Zanker (1997) noted that the visual field of fiddler crabs is divided into three zones. The lower field represents objects smaller than the crab. Objects in the dorsal visual field correspond to everything larger that the animal including predators and the waving claws of conspecifics. The equatorial field of view, a narrow 10° horizontal slice of the visual field, picks up everything five body-lengths or more away, and is the most visually acute of the three distinct

fields. Villanueva (1982) found that the purple shore crab, *Hemigrapsus nudas*,

possesses seven visual neuronal elements including fibers sensitive to moderate

motion, slow motion, fast motion, approaching movement, light level, and visual

processing. Fiddler crabs responded to visual cues of light intensity (Hyatt,

1974), color (Hyatt, 1975), and motion (Hemmi, 2005a). Behavioral evidence

suggests that the symbiotic crab, *Allopetrolisthes spinifrons*, uses color vision

(Baeza & Stotz, 2003).

Mangrove climbing crabs, *Sesarma leptosoma*, used visual information to

recognize predators (Cannicci*, et al.*, 2002) and to migrate daily up and down

mangrove trees (Cannicci*, et al.*, 1996). The hermit crab, *Clibanarius vittatus*,

were significantly attracted to silhouettes in the shapes of horizontal rectangles,

horizontal diamonds, squares, semicircles, and triangles, but not to vertical

rectangles or vertical diamonds (Diaz*, et al.*, 1994). When exposed to pairs of

these shapes, the most attractive shape overall was the horizontal rectangle

while the least attractive was the vertical diamond. Hermit crabs oriented poorly

to the shape of suboptimal shells but oriented very well to shapes that

represented more optimal gastropod shells (Diaz*, et al.*, 1994). There is some

evidence that hermit crabs can visually discriminate between shell species

(Hazlett, 1982; Diaz*, et al.*, 1995).

Chemical

Olfaction is the detection of chemical cues dissolved in air or water, while

taste is the detection of cues by direct contact. The number of crustacean

chemosensory neurons can number in the millions (Derby & Steullet, 2001) and

while the majority are located on the two pair of antennae, other locations such as maxillipeds and pereiopods are also chemosensitive. Having multiple sensors facilitates: 1) extending the sampling surface area of the animal, 2) increasing the range of stimuli detected, 3) increasing the sensitivity and resolution of detection, 4) maintaining sensory function in case of damage, and 5) enabling specialized central processing centers (Derby & Steullet, 2001). In crustaceans, sensilla are receptor neurons packaged into cuticular extensions (Mesce, 1993b; Derby, *et al.*, 2001). Aesthetasc sensilla (found only on the distal half of antennular flagella) are chemosensory (Derby, *et al.*, 2001) whereas other sensilla are chemo-mechanosensory (Derby & Steullet, 2001). Many crustaceans (lobsters, crabs, crayfish) have been shown to reliably orient to odor sources 2 m away in lab flumes (Derby, *et al.*, 2001).

The effect of chemical cues can be observed in the change of behavior concomitant with adding specific chemical cues or odors. In general, the physiological responses to chemical compounds parallels the behavioral responses observed in animals (Corotto, *et al.*, 2007). Chemical cues have been demonstrated to strongly influence foraging behavior in crustaceans, even in the absence of visual and tactile cues. For instance, in the rock crab, *Cancer irroratus*, decaying prey odor had a significant effect on foraging behavior in the dark, but odor of live mussels alone did not (Salierno, *et al.*, 2003). The California spiny lobster, *Panulirus interruptus*, locomoted spontaneously at night, and low concentration chemical cues were used for near search rather than long distance attraction (Zimmer-Faust & Case, 1983). Steele, *et al.* (1999) found that

crayfish behaved with dichotomous responses to chemical cues. Whereas low

concentrations induced distant food-search through locomotion, high

concentrations activated substrate probing. Crayfish oriented to baits that

emitted fish odor, but not to baits similar in shape and texture without chemical

cues (Moore & Grills, 1999).

Chemical cues can also be used for orientation. Diaz, et. al. (1999) found

that juveniles of the blue crab, *Callinectes sapidus*, used chemical cues for

dispersal in estuaries. Stage I instars oriented away from solid objects in the

presence of offshore water, while stage IV-V instars swam away from 90^0 objects

and toward 270^0 targets in both offshore and estuary water (Diaz*, et al.*, 1999).

Juvenile spiny lobsters, *Panulirus argus*, were recruited to dens by conspecific

odors without any other visual, tactile, or auditory cues (Nevitt*, et al.*, 2000).

Chemical cues that indicate the presence of a predator can include both

direct and indirect cues. Direct cues are produced by the predator, while indirect

cues are produced from alarmed, injured, or dead conspecifics (Dicke & Grostal,

2001). For some crabs, such as *Aratus pisonii* and *Uca cumulanta*, attraction to,

and orientation toward, shelter objects increased when predator odors were

presented (Chiussi, 2002; Chiussi & Diaz, 2002). The anti-predator response of

hermit crabs includes two behaviors, taking refuge and fleeing. Mima, *et al.*

(2003) found that the hermit crab, *Pagurus filholi*, in lighter weight shells were

more vulnerable to predation than hermit crabs in heavier shells, and that they

spent less time frozen and fled faster in the presence of either predator odor or

injured conspecific odor than they did in plain seawater. When predator odor

was presented to the hermit crab, *Clibanarius vittatus*, it grasped shells less and fled more than when no predator odor was present (Rittschof & Hazlett, 1997).

Specific chemical cues are used by hermit crabs to locate available shells. In hermit crabs, like *Clibanarius antillensis, C. vittatus*, and *Pagurus longicarpus,* chemical cues of predators, dead gastropods, dead conspecifics, and calcium shells increased orientation toward shell-shaped objects (Orihuela*, et al.*, 1992; Chiussi*, et al.*, 2001; Gherardi & Atema, 2005; Tricarico & Gherardi, 2006). The hermit crab, *Pagurus longicarpus,* could discriminate different sources and meanings of chemical substances. Hermit crabs remained motionless when presented with dead conspecific odor, but initiated shell investigation when presented with the odor of live conspecifics (Gherardi & Atema, 2005). Rittschof (1982) studied the effect of adding bivalve, gastropod, and crab flesh to tidepools. Flesh consumers were attracted in the first 12 hours, while shell users were attracted for up to several days. Not only can crustaceans discriminate between odor sources, but they behave as though they attach specific meaning to these discrete odors.

The hydrodynamics of a habitat can have large effects on both the chemical signal dispersion and the behavior of animals therein. Moore and Grills (1999) conducted orientation experiments in a flow-through artificial stream and found that although there was no difference in crayfish maximum walking speed across sand or pebble substrates, crayfish walked faster on cobblestone than on sand in response to chemical (fish) cues. Crayfish were more accurate in orienting to the fish gelatin on cobblestone (100%) compared to sand (77%

accuracy). Perhaps chemical cues were easier to follow due to the turbulence caused by cobble than when chemical cues flowed smoothly over sand. Hydrodynamics may constrain the olfactory ability of some organisms and may therefore play a role in habitat selection (Moore & Grills, 1999). Antennular flicking and leg waving may be examples of similar chemosensory behavior used to increase the sensitivity of setae by increasing the movement of fluids across the setae (Mesce, 1993b). Olfactory signals become more important when vision is impaired due to environmental conditions such as water clarity or darkness (Moore & Bergman, 2005).

Tactile

Tactile cues are here defined as information gathered while in contact with an object. Tactile information can include chemosensory cues or "taste" (Dicke & Grostal, 2001), as well as mechano-sensory cues such as shape, size, texture, and weight information (Elwood & Neil, 1992:56).

Although appendages, including walking legs and mouthparts, are most often used to gain tactile information, antennules can also be used by crustaceans to detect tactile and chemical signals (Moore & Bergman, 2005). Chemo-mechanosensory sensilla in crustaceans include hair pegs, hedgehop sensilla, fringed sensilla, hooded sensilla, and simple sensilla (Derby & Steullet, 2001). Bi-model sensilla are useful for identifying the spatial location of chemo-tactile stimuli. Further evidence of the tactile nature of these chemo-mechanoreceptors are their location; hedgehog and fringed sensilla are only found on the distal two segments of some legs (Derby & Steullet, 2001). Some

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evidence suggests that mechanoreceptor neurons in bimodal sensilla on the antennules project to the same neuropils as the chemoreceptor neurons (Derby & Steullet, 2001).

Mesce (1982) demonstrated that it was the calcium present on the surface of shells that elicited shell investigation behavior in the hermit crabs, *Pagurus samuelis* and *P. hirsutiusculus*. Although they preferred objects with high calcium levels, when seawater was saturated with calcium, masking the calcium cues of the shell, hermit crabs preferred natural shells over calcium rich plaster ($CaSO_4$) shell replicas. Hermit crabs possibly use shell shape, texture, and weight information in choosing shells, and must rely more heavily on these features when calcium cues are obscured. For the hermit crabs *Pagurus hirsutiusculus* and *P. samuelis*, chemical cues of shell presence were detectable in the dark only when hermit crabs were within 1 cm of the shell (Mesce, 1993a). In addition, both species were able to find and occupy buried shells every time when uncoated with the calcium cue present, but never found them when shells were coated.

Once a hermit crab comes into contact with a shell, it probes and scrapes the shell in an exploratory behavior (Mesce, 1993a). The appendages, especially the minor cheliped of *Pagurus hirsutiusculus*, are extremely setaceous, which may be the location of the calcium and tactile sensory structures (Mesce, 1993a). The minor chelae also possess simple setae (sensilla) and chelar teeth that are mechanosensory in function. Moving appendages across the shell surface may splay apart the chemosensitive setae with dense tufts to expose them to

chemical stimulation during tactile investigation (Mesce, 1993a). Contact calcium

reception distinguishes shells from other objects, such as rocks. Although the

antennal sensilla and antennular aesthetascs function primarily as chemosensory

organs, chelar structures sensitive to calcium may also serve to detect peptides.

Both antennae and chelipeds are used in shell detection.

Crustaceans possess the necessary sensory organs and neural structure

to utilize visual, chemical, and tactile information in decision making.

Decision Hierarchies

Much of the current crustacean research has evaluated the influence of

only one or two stimuli on behavior. Although visual, chemical, tactile, and

possibly other cues, are capable of being perceived by crustaceans, they are

seldom tested in experiments congruently.

Information Processing

As I have discussed, animals in general, and crustaceans in particular, are

capable of perceiving a wide range of stimuli. Reception, the taking in of

information, is the first stage in cognition (Dukas & Real, 1993), and attention, the

limiting of information processed, is the second stage. Having millions of sensory

neurons, crustaceans likely are restricted in the quantity of incoming sensory

data that can be processed or acted on at once. Presumably, animals attend to

only one or two sensory modalities at a time. When focusing attention narrowly

on one sensory cue, processing time can be reduced thereby increasing the rate

of decision-making. I here define "decision hierarchy" as the relative ranking of

sensory modalities such that one modality has a stronger influence on a specific behavior than other senses perceived.

Sequential Decision Hierarchies

Schöne (1964) used the terms "releasing mechanism" to describe the specific stimulus that initiates a behavior pattern and "directing mechanisms" to describe the stimuli that influence steps of execution of the behavior. For example, in conditioning experiments an animal must first associate the stimulus of the starting location in a maze with the task of acquiring a reward, and then they must associate various orientation cues with the correct maze pathway. The use of separate cues to initiate and control discrete steps in behaviors implies stimuli are arranged in a step-wise decision hierarchy.

I will use the term "Sequential Decision Hierarchies" (SDHs) to describe the use of specific sensory cues in the execution of a series of discrete steps in a behavior. During the use of SDHs, one stimulus initiates the first behavior, another cue initiates the second behavior, and so on until the task is completed. Table 1 summarizes examples of SDH in various taxa.

Esch, *et al.* (2002) described a series of behavioral choices in the medicinal leech, *Hirudo medicinalis*, in which the decision to initiate a task was made before the decision of what form of the behavior to use in accomplishing the task. Stimulation of mechanoreceptors in the leech's posterior activated R3b1 neurons that produced elongation, which in turn either activated swimming inter-neurons if in deep water or activated crawling contractions if in shallow water (Esch*, et al.*, 2002).

Physical gradients and discontinuities such as light, pressure, turbulence, currents, temperature, and salinity have all been implicated in gelatinous zooplankton aggregations and migrations. Usually the diurnal vertical migration (DVM) pattern of jellyfish is upward to the surface at night and downward away from the surface during the day. Graham, *et al.* (2001) proposed that changes in light intensity at dawn may provide the cue to initiate downward swimming, but a secondary cue such as pressure, temperature, or salinity may determine the depth of the migration. In several marine lakes in Palau, two species of scyphomedusae exhibited different DVM patterns. *Aurelia aurita* engaged in the typical DVM, swimming to the surface at night, even though there were no pelagic predators in these lakes. Until the recent disappearance of *Mastigias* sp. jellyfish from the Eil Malk Jellyfish Lake in Palau, they engaged in a DVM that was the reverse of *A. aurita* in that lake. *Mastigias* migrated to the sunlit surface waters during the day and engaged in horizontal migrations following the path of the sun to provide the symbiotic zooxanthellae with light for photosynthesis (Graham, *et al.*, 2001). These jellyfish exhibited flexibility in the sequence of cues eliciting migration. In *Mastigias* sunlight was the cue to ascend to the surface, and in *Aurelia* sunlight was the cue to descend.

Crustaceans also demonstrate the use of SDHs in both homing and foraging tactics. Cannicci, *et al.* (2000) tested whether the swimming crab, *Thalamita crenata*, could remember relative position of landmarks using a cognitive map. After three weeks of conditioning to landmark bricks painted red, green, blue, and yellow near their home dens, both the landmarks and swimming

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crabs were moved both 5 m and 80 m away.   In the near home shift, swimming

crabs were able to use both the landmarks and other features to correctly find the

new position of the den. In the far displacement experiment, swimming crabs

were strongly disoriented during the first half of the path, looping back and forth,

but took a direct route to the den in the second half. This implies the sequential

use of separate cues for each portion of the journey. During crustacean feeding

behaviors, different chemosensors may act sequentially: antennae initiate

searching; leg chemoreceptors control grasping; and mouthpart chemoreceptors

mediate ingestion (Derby*, et al.*, 2001).

Thus, SDHs serve to focus animal attention on a specific cue or condition

at each stage of a behavioral sequence. Having discrete behavioral units

controlled by separate cues gives the flexibility to modify and correct actions at

each change of behavioral segment.

"Contextual Decision Hierarchies"

Recently, Billock and Dunbar (submitted-b), have developed the concept

of "Contextual Decision Hierarchies" (CDHs), which occur when various sensory

modalities are ranked in order of influence on a single behavior. CDHs enable

animals to direct their attention to a single sensory modality during a behavior,

yet maintain the flexibility to switch to a secondary or tertiary stimulus if the

primary one is unavailable or ambiguous.

The specific context of a CDH may arise internally from an individual's

motivation to seek a resource, or externally from changes in environmental

conditions. CDHs can provide several benefits. First, by focusing attention on a

primary cue, accurate decisions can be made quickly and reliably at each

occurrence. Second, by utilizing a hierarchy, secondary information from other

sensory modalities can still be accessed when the primary cue is absent or

ambiguous, i.e. switching from visual to olfactory cues in the dark. Lastly,

secondary cues may act synergistically in reinforcing or modifying cues, though

may not themselves be necessary for eliciting that behavior. Shettleworth (2001)

noted that for some animals, discrete stimuli compete for control of behavior such

that one stimulus overshadows the other in directing behavior, but alone a

secondary stimulus can still elicit a response. CDHs effectually combine the

cognitive processes of attention (Dukas & Real, 1993) and contextual modulation

(Shettleworth, 2001). Most behavioral models incorporate some degree of

hierarchy, or asymmetry of influence between stimuli on behaviors. The

hierarchical interaction may be all-or-nothing or a modulation of one behavior by

another input. Stimuli, motivation, and experience may all influence behavior

patterns (Hazlett, 1996a). Various research with both vertebrates and

invertebrates, summarized in Table 2, has shown that when sensory cues are

presented separately and in combination to animals, a sensory hierarchy is used

to preferentially sort information.

The tadpoles, *Rana lessonae* and *R. esculenta*, were tested by Stauffer

and Semlitsch (1993) for predator avoidance responses using factorial

combinations of visual, chemical, and tactile cues. Tadpoles responded most

strongly to treatments that included chemical cues, and adding tactile information

increased the response. Perhaps tactile cues provide additional information

about the predator, such as direction, but are inconsequential by themselves. Stauffer and Semlitsch (1993) suggested that it would be too costly to respond to all tactile stimuli (motion in the water) without an appropriate chemical cue signaling danger.

Persons and Uetz (1996) tested the influence of visual and vibratory cues on patch residence time in the wolf spider, *Schizocosa ocreata*. Their results demonstrated that foraging behavior in wolf spiders is influenced more by visual than vibratory cues. Although vibratory cues were not important when presented alone, they significantly increased foraging time when paired with visual cues.

Bees appear to use CDHs for orientation. Bees transported to a remote and unfamiliar site will ignore landmarks and orient to sun compass cues until landmarks are prominent enough to indicate that such a choice would be wrong (Menzel*, et al.*, 1998). Many animals have redundancy in their navigational systems and may thus switch to secondary cues depending upon conditions. For example, bee eyesight is relatively poor, equivalent to 20/2000 human vision, and yet they routinely use landmarks to find their hive and food sources (Gould, 2002). In all likelihood, bees switch between route memorization and landmark use as needed.

Contexts such as location, light illumination, and time of day have all been demonstrated to influence the foraging decisions of bees. Bees have been trained to associate patterns with location, and will choose the correct geometric pattern at a given location (Collett*, et al.*, 1997), or the correct flower color at a specific location (Collett & Kelber, 1988). Bees can also associate the context of

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light color and illumination level, both of which are environmental cues, with specific flower colors for foraging (Lotto & Chittka, 2005). In addition, bees can associate time of day with flower color and correct position to land on a flower (Gould, 1987).

Rebach (1981) has proposed that although animals can perceive a wide range of cues, some information has a stronger influence on orientation than other cues, and that cues may be arranged hierarchically, such that when the primary cue is unavailable, secondary cues are used for navigation. The fiddler crab, *Uca cumulanta,* uses orientation cues of sun position, beach slope, and shore landmarks during homing behavior. Chiussi and Diaz (2001) found that celestial cues (sun position) served as the primary cue, with beach slope and shore landscape operating as secondary cues. In the absence of celestial cues (cloudy days), slope or landscape was used to determine shoreward direction. When crabs were transplanted to a beach facing 180º opposite of the home beach, celestial cues overrode landscape cues, causing crabs to orient away from the shore even though it was in opposition to landscape information at the transplantation beach. For an animal living in the intertidal zone with consistent access to celestial cues, sun position would be the most reliable cue to use for orientation. Slope and landscape cues are used to reinforce the celestial cues, or can be used as backup cues when the sun is obscured during cloudy days. Chiussi & Diaz (2001) suggest that animals may be adapted to respond strongly to the most reliable cue, and less strongly to stimuli that are subject to random change.

Billock and Dunbar (submitted-b) found that the hermit crab, *Pagurus samuelis*, utilized tactile information over chemical and visual cues when searching for shells. In contrast, when searching for 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.

For the hermit crab *Clibanarius vittatus*, the number of shell grasps is reduced and locomotion increased when predator odor is added to the odor of conspecific blood, snails, or fish (Hazlett, 1996a). Perhaps contexts are also arranged hierarchically based on level of effect on survival. Hermit crabs respond to stimuli in an apparent order of importance, with predator cues overriding food availability cues, which in turn override shell availability cues (Hazlett, 1996a; Rittschof & Hazlett, 1997). Predator odor effectively inhibits both feeding locomotion and shell acquisition grasping (Hazlett, 1996a). For hermit crabs, predation risk can be immediate, the risk of death by starvation may take days or weeks, and the effects of an ill-fitting shell may not be felt for several weeks, or even months. Billock and Dunbar (submitted-a) found that when hermit crabs are both starved and removed from shells, they preferentially seek shells over food.

When a brachyuran crab, *Matuta lunarus*, was presented with varying strengths of predator odor with a constant feeding cue, the decaying snail odor elicited shell grasping and increased locomotion until the predator odor level was increased to 10 % or higher (Hazlett, 1997). When food and predator odors were presented together to the crab, the combination of chemical cues elicited an

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increase in locomotion compared to predator odor presented alone (Hazlett, 1997).

The hermit crab, *Pagurus longicarpus,* in inadequate shells has a stronger response to dead gastropod odor than it does to live gastropods, alive or dead conspecifics, or seawater. However, in the presence of dead conspecific odor, hermit crabs will remain motionless regardless of shell fit (Gherardi & Atema, 2005). Behavioral response to chemical cues are mediated by both internal context (lacking a shell) and external context (predator cue) indicating the ability to make context-specific behavioral choices.

From these vertebrate and invertebrate examples, the importance of specific stimuli in directing behavior emerges. Since these taxa are capable of perceiving multiple types of sensory information, yet they react to only one or two cues during a given behavior, I suggest that they are utilizing CDHs.

CDH Model

Between behavior sequences, animals may monitor the environment through all sensory modalities (see Figure 1). However, when an animal becomes aroused because the internal and/or external context(s) has changed, it makes the decision to initiate a behavior. This primes the nervous system to become more sensitive to one sensory modality while other modalities decrease in influence. At this point, the CDH is activated and attention turns to the primary cue. However, if the primary cue is obstructed, such as loss of vision at night, the secondary cue increases in importance. In this way, either using the primary or secondary stimulus, the animal completes the behavior. Although primary cue

loss may lengthen the time necessary for behavior completion, secondary cues can still be effectual.

While the underlying mechanisms involved in decision hierarchies are unknown, hormones, neurons, and neural processing centers are no doubt involved. Monoamines may alter the activity of decision-making centers and serve as a link between information gathering and decision making via short-term priming of the nervous system in specific situations (Briffa & Elwood, 2007). Biogenic amines such as serotonin, octopamine, norepinephrine, and dopamine have all been implicated in the control of aggression in animals (Huber*, et al.*, 1997a; Huber*, et al.*, 1997b; Moore & Bergman, 2005). Some research suggests that crustaceans may have two types of 5-HT receptors that mediate short and long term memory (Aggio*, et al.*, 1996).

Briffa & Elwood (2007) found that circulating monoamines modulated decisions during hermit crab shell-fights; attackers had higher 5-HT levels than defenders, and shell-fight winners had lower dopamine levels than those which did not fight. In crustaceans, 5-HT has been shown to up-regulate the activity of abdominal muscles in the crayfish, *Procambarus clarkii* (Yeh, *et al.*, 1996), and the hermit crab, *Pagurus bernhardus* (Briffa & Elwood, 2007). Attacking hermit crabs used their abdominal muscles to perform shell-rapping against the opponents shell. Dopamine may be related to hermit crab attack motivation but not the subsequent decision of how vigorously to fight (Briffa & Elwood, 2007).

Briffa and Elwood (2002) found that if an attacker had high lactate concentrations, or if the defender had low glucose levels, the outcome was more

likely to be in favor of the attacker. Likewise, they found that successful attackers generally rapped with a higher temporal rate and stronger intensity than unsuccessful attackers. The current physical state of the combatants provided the motivation that determined their behavior.

Esch*, et al.'s* (2002) work with leeches has demonstrated the interplay between information received by receptor neurons and the control of behaviors such as locomotion by muscle neurons.

While the proximate cause of CDH is physiological, the ultimate cause must be through increased survivability and fecundity. Burghardt (2002) has shown that the ability to learn specific cues associated with feeding is heritable. In addition, Dukas & Bernays (2000) have demonstrated that learning to associate color, taste, and location (visual, chemical, and tactile cues) with food quality improves growth rate.   Some species occur across a wide and varied range, so the most reliable cue that becomes primary for a CDH may be a compromise of general cues at the expense of more informationally rich, but less widely accessible cues. Contextual Decision Hierarchies allow animals to make the best possible decision based on the information available at a specific time or location.

Future of CDH Research

Understanding the way in which animals utilize information about their environment would be a benefit in planning appropriate conservation measures. Species that rely heavily on one cue at the exclusion of other potential

information are at higher risk of suffering ill effects, than species that have flexible decision hierarchies. For instance, it has been proposed that cetacean mass beachings may be a result of anthropogenic sonar (Fernandez*, et al.*, 2005).   Reliance on sonar navigation, at the exclusion of other possible stimuli, may contribute to the beaching problem. In organisms that have secondarily lost a sensory modality, as is common in troglomorphy or "cave syndrome", the reliance upon a secondary cue has become permanent. Blind cave fish appear to use cognitive maps of their location by memorizing the features of the cave using their lateral line (Teyke, 1989). The blind river dolphin, *Platanista gangetica*, uses sonar and tactile cues obtained from the fins and rostrum that make contact with the substrate while side-swimming (Herald*, et al.*, 1969). Research with animals that have restricted sensory apparati may also lead to fruitful insights into the importance of Contextual Decision Hierarchies.

Additionally, the CDH model may bring new insight into the sensory processing mechanisms of various taxa. Comparative research that elucidates the difference in information handling among organisms could prove fruitful. Although this review has focused on crustacean examples of CDHs, other examples of CDHs warrant exploration of stimuli processing in higher taxa.

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Table 1. Summary of Sequential Decision Hierarchies found in a range of taxa.

Species	1st Stimulus/ 1st Behavior	2nd Stimulus/ 2nd Behavior	Source
Medicinal leech *Hirudo medicinalis*	mechanoreceptors/ elongation	water level/ swimming or crawling	(Esch, *et al.*, 2002)
Jellyfish *Aurelia aurita*	sunlight/ initiate descent	water pressure/temp/ stop descent	(Graham, *et al.*, 2001)
Honey bee *Apis mellifera*	flight distance/ how long to fly	landmarks/ when to stop flight	(Chittka, *et al.*, 1995)
Leaf-cutter bee *Megachile rotundata*	visual cues/ locating nest	edge lengths/ locating nest opening	(Fauria, *et al.*, 2004)
Crustaceans	antennae chemo-reception/ initiate food searching	leg chemo-reception/ food grasping	(Derby, *et al.*, 2001)

Table 2. Summary of Contextual Decision Hierarchies found in a range of taxa.

Species	Behavior	Primary Cue	Secondary Cue	Source
Frog *Rana lessonae*	anti-predator	chemical	tactile	(Stauffer & Semlitsch, 1993)
Wolf spider *Schizocosa ocreata*	foraging	visual	vibratory	(Persons & Uetz, 1996)
Bees *Apis mellifera*	homing	sun compass	landmarks	(Menzel, *et al.*, 1998)
Fiddler crab *Uca cumulanta*	homing	sun position landmarks	beach slope &	(Chiussi & Diaz, 2001)
Hermit crab *Pagurus samuelis*	shell seeking	tactile	visual/chemical	(Billock & Dunbar, submitted-b)
Hermit crab *Pagurus samuelis*	foraging	chemical	tactile/visual	(Billock & Dunbar, submitted-b)

Figure 1. Diagram of Contextual Decision Hierarchy model. The circle
represents the sensory modalities that are available and monitored
between activities. Light arrows indicate steps in the process and dark
arrows indicate the influence of contexts. When internal or external
contexts change, the decision can be made to initiate a behavior which in
turn establishes a specific hierarchy unique to that behavior (CDH).
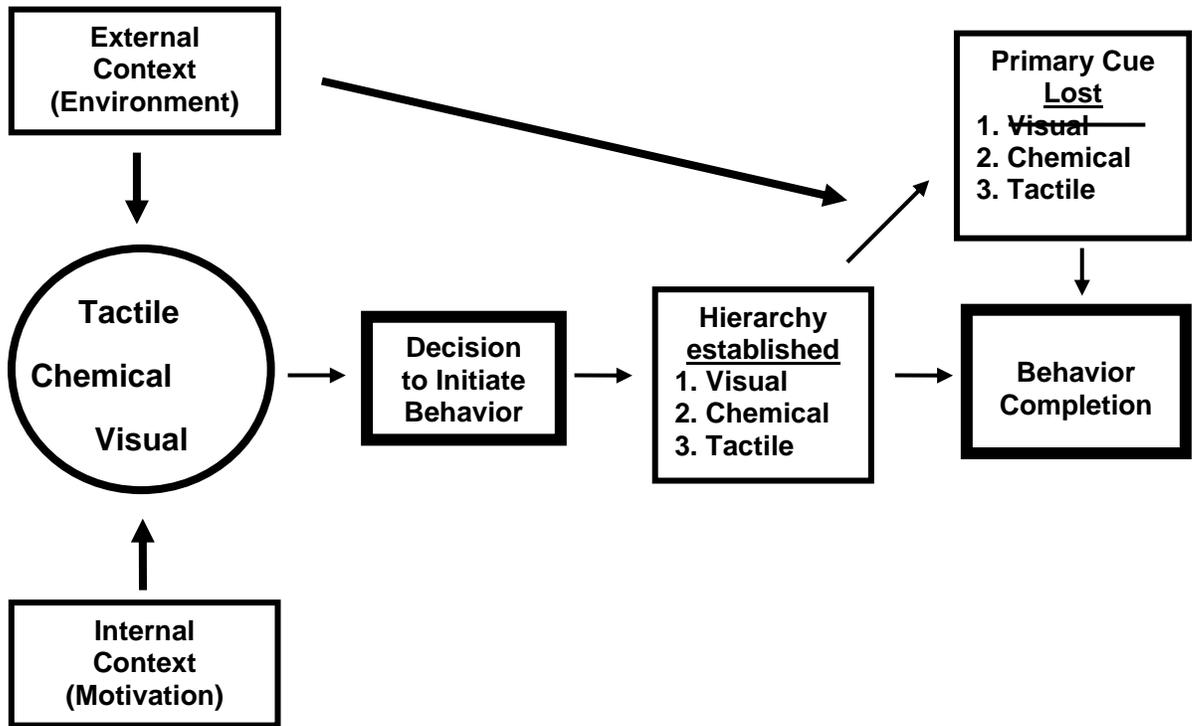
CHAPTER III

Influence of Motivation on Behavior in the Hermit Crab, *Pagurus samuelis*

Wendy L. Billock and Stephen G. Dunbar

Abstract

Both the need for shelter and the need for food can be motivations that alter animal behavior. We tested the hypothesis that the hermit crab, *Pagurus samuelis*, deprived of food, shells, or both will respond differently from control hermit crabs when presented with food and shells concurrently. We measured the number of contacts made with both food and shells, and time elapsed until hermit crabs either began feeding or inserted into shells. We interpret making few contacts and initiating behavior quickly to be an indication of short decision time and high motivation; whereas, making many contacts and having long initiation time indicates a long decision time and low motivation to acquire resources. Control (C) hermit crabs made 72 % more contacts with food and 53 % more contacts with shells than shell-less (S) crabs. Control hermit crabs also made 34 % more contact with food and 35 % more contacts with shells than starved and shell-less (StS) hermit crabs. This suggests that shell-less hermit

crabs were more motivated to acquire shells than control crabs. In addition,

shell-less hermit crabs chose to insert into provided shells, while hermit crabs

remaining in their shells chose to feed.   Results indicate that being shell-less is a

stronger motivation than being starved, such that finding shelter takes priority

over finding food when both are needed. In rocky intertidal environments,

resources such as food and shells are likely to be ephemeral. Hermit crabs that

are motivated to make appropriate decisions to acquire specific resources have

an advantage over those that are distracted by numerous objects in their

environment.

Introduction

Optimization models of feeding and predator avoidance behaviors predict

that there are trade-offs necessary to maximize fitness, such that the stronger the

motivation to feed, the more risky the animal's behavior (Krebs & Davies, 1993).

Hermit crabs make an ideal model animal for motivational studies (Elwood, 1995)

because of their need to acquire both food and shell resources. In nature, shells

are often limiting, so most hermit crabs occupy suboptimal shells (Elwood & Neil,

1992; Halpern, 2004) and will readily investigate and switch to new shells when

encountered (Abrams, 1987). Most hermit crab species are omnivorous

detritivores that occasionally feed on macroscopic animal and plant material

(Hazlett, 1981). Windfall food opportunities, such as a recently killed gastropod,

occur only occasionally but will readily draw hermit crabs to the site (Rittschof,

1982; Elwood & Neil, 1992; Hazlett*, et al.*, 1996).

Hermit crabs have been used in a variety of experiments to elucidate the role of motivation on behavior. Reese (1963) demonstrated that hermit crabs in suboptimal shells showed higher motivation to acquire shells than crabs in preferred shells; and shell-less hermit crabs were more motivated than crabs in suboptimal shells. Elwood (1995) found that the motivational state can be identified by the length of time hermit crabs spend examining a prospective shell and the duration of the startle or immobilization response, following cues of predator presence. The readiness to initiate a shell-fight with another hermit crab and the decision to continue fighting are also measures of motivation to acquire a better shell (Elwood, *et al.*, 1998; Gherardi, 2006). In addition, the length of time a crab tries to access a shell with a blocked aperture can indicate the motivation to exchange shells (Elwood, 1995). Both the need for a shell and the need for food can be motivations that alter hermit crab behavior.

Although external cues of resource availability may be perceived equally by conspecifics, the internal state, or motivation, of the receiver can cause individuals to respond quite differently to the same information. Internal factors affect the motivational state of an animal and the motivational state determines the strength (intensity and completeness) with which a behavior is carried out (Tinbergen, 1951; Reese, 1963). Tinbergen (1951) suggested three methods of measuring motivation: changes in the intensity or frequency of responses to a constant condition; the minimum intensity of a stimulus necessary to initiate a response; or the minimum intensity of a stimulus required to inhibit a reaction.

While it has been demonstrated that hermit crab motivational level can be measured through persistence in either shell or food acquisition behaviors, the interaction between two motivations, the need for food and shells, is not well understood. Some research has been done with hunger and shell inadequacy interactions (Hazlett, 1996; Hazlett, 1997; Rittschof & Hazlett, 1997), but to our knowledge no studies have addressed the issue of hunger and shell-lessness conjointly. The purpose of this research is to determine if hermit crab motivation, based on current physical need, initiates a specific behavior pattern at the expense of another, and if one motivation can override another. Our experiment utilized the first of Tinbergen's three methods; measuring changes in hermit crab responses to the simultaneous presentation of two resources. We tested the hypothesis that hermit crabs deprived of food, shells, or both will respond differently from control hermit crabs when presented with food and shells concurrently. This was measured by time to first contact with the resource, number of contacts, time to initiate behavior, and final behavioral choice.

Materials and Methods

Animal collection and maintenance

The hermit crab, *Pagurus samuelis* (Stimpson), was collected from Little Corona del Mar, Newport Beach, California (33°35.36'N, 117°52.09'W) in November 2007 and maintained in the laboratory at 23 - 24° C with ambient light.

Hermit crabs were divided into four groups of forty animals (N = 160). In the control group (C), crabs were provided extra shells in the holding aquarium

and fed shrimp to satiation prior to testing. Control crabs were left in their shells

during testing. In the shell-less group (S), crabs were fed shrimp to satiation, but

were removed from their shells prior to testing. In the starved group (St), crabs

were starved 8 – 15 days because tests began on day 8 post-feeding and were

spread over a 7 day period. Group St was also provided with extra shells to

choose from prior to testing. In the combination starved and shell-less group

(StS) crabs were starved 8 – 15 days and removed from their shells prior to

testing. Hermit crabs were tested only once.

Test Protocol

Each hermit crab was measured for shell aperture width and length, and

wet weight including shell. After removal from the shell, either prior to, or

immediately after testing (see Table 1), we also measured crab body weight and

shield length. Shell and hermit crab measurements were used in a linear

regression to determine preferred shell size to offer during testing.

The experimental arena was a 21.5 cm diameter Plexiglas cylinder

covered in white Mylar to make it opaque. 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). The only light source during sessions was a Philips brand 40 Watt

"Natural Light" bulb suspended 30 cm above the test arena. A green light was

used near the video monitor so notes could be written, while a black curtain

surrounded the arena to obscure any researcher movements from test hermit

crabs. Between each test, the arena was rinsed with soapy water to ensure that

no traces of chemical cues remained in the arena for subsequent test sessions.

During test sessions, 500 ml of seawater was added to the arena and both

an appropriately sized *Tegula funebralis* (A. Adams, 1855) shell (within 1.25 mm

of the hermit crab's preferred shell aperture width) and a piece of shrimp tissue

($0.20 \pm .01$ g) were placed equidistant apart from the starting position of the

hermit crab and 1 cm from the arena wall. Shell and shrimp positions were

alternated between tests. In the S and StS treatments, hermit crabs were

removed from their shells using a table vise. Each hermit crab was placed under

a plastic box ($2 \times 2 \times 1.5$ cm) until the test began and the box gently lifted by a

pulley. When the box was lifted, we measured the time to first contact with the

objects, as well as the total time elapsed before either insertion into the shell or

initiation of feeding. During each test session we recorded the following

measurements: first object touched; time to first contact with both shells and

food; number of contacts with each object; and which behavior was exhibited

(feeding or inserting into shell). Sessions ended when crabs decided to feed or

insert into shells. If a hermit crab took the maximum time of 15 minutes without

choosing to feed or insert, it was scored as 'neither' behavior. Ten replicates

were conducted for each treatment (see Table 1), and each treatment was

repeated four times.

Statistics

All statistical analyses were run using the Statistical Package for the

Social Sciences (SPSS). Pearson's chi-square tests were used to compare

differences between treatment groups in the first object touched (food or shell) and the behavior exhibited (feed, insert, or neither). To compare the time to first contact, number of contacts, and decision time, 2 × 4 ANOVAs were used, with object (food or shell) treated as a within-subjects factor and condition treated as a between-subjects factor with four levels (C, S, St, and StS). Scheffe's post-hoc tests were conducted to determine if any treatments were significantly different from each other. Independent t-tests were used to determine if there were significant differences in the mean time to contact and the mean number of contacts between food and shells. A stepwise multiple regression was conducted to determine which independent variable (shell weight, shell aperture width or aperture length) was the best predictor of hermit crab weight.

Results

A stepwise multiple regression of shell attributes (shell weight, aperture width, and aperture length) revealed that aperture width is the best predictor of hermit crab weight ($R^2 = 0.751$, $F_{1,150} = 458.39$, $p < 0.001$; Aperture width = 0.22 + 0.18 × Body weight). The resulting regression (Figure 1) was used to determine what size shell to offer each hermit crab during test sessions.

There was no difference between treatments in the first object touched by each hermit crab ($\chi^2 = 0.440$, df = 3, $p = 0.932$). Although shells were contacted first more often than food (see Table 2), this difference was not significant.

ANOVA results of mean time to initial contact with each object showed no significant main effect for either object ($F_{1,225} = 2.803$, $p > 0.05$) or treatment

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($F_{3,225}$ = 1.858, p > 0.05, see Figure 2). Interactions between factors were also not significant ($F_{3,225}$ = 2.303, p > 0.05). An independent t-test revealed that in group C, the mean time to initial contact with shells was significantly shorter than the mean time to contact with food (F = 12.04, df = 65, p < 0.01).

A two-way ANOVA was conducted to investigate differences in the number of contacts made by hermit crabs given two objects concurrently (shell and food) and randomly subjected to one of four treatments. Three hermit crabs in the C group and one hermit crab in the St group, had contact values that were extreme outliers and were therefore excluded from the analysis. ANOVA results showed significant main effects for both objects ($F_{3,304}$ = 16.014, p < 0.001, partial η^2 = 0.09) and treatment ($F_{3,304}$ = 9.705, p < 0.001, partial η^2 = 0.05). Interactions between factors were not significant ($F_{3,304}$ = 0.642, p > 0.05). Calculated effect size for each factor indicates a small proportion of contact variance is accounted for by each factor. A Scheffe's post-hoc test revealed that group C was significantly different in number of contacts from group S (p < 0.001) and group StS (p < 0.001), see Figure 3. In addition, group St was not significantly different from groups S or StS (p > 0.05). A t-test revealed that in group S, the mean number of contacts with food was significantly lower than the mean number of contacts with shells (F = 17.87, df = 78, p < 0.001).

Two-way ANOVA results of mean time to initiate the chosen behavior show no significant main effects for either objects ($F_{1,142}$ = 0.003, p > 0.05) or treatment ($F_{3,142}$ = 0.413, p > 0.05), see Figure 4.

Treatment significantly affected the final behavior exhibited by hermit crabs (χ^2 = 114.67, df = 6, p < 0.001). Hermit crabs in the C and St groups chose to feed while crabs in the S and StS groups chose to insert into shells (see Table 3). All group S crabs chose to insert into shells and none chose to feed. In group C, 5.0 % chose to switch shells and in group St, 8.0 % chose to switch shells (see Figure 5). In the StS group, while 77.5 % chose to insert into shells, 17.5 % chose to feed even without a shell. Over all, 10 of 160 hermit crabs neither fed nor inserted into a shell during the 15 minute sessions.

Discussion

In hermit crabs, motivation by food or shell deprivation significantly affected which behavior was exhibited. Hermit crabs removed from shells were more likely to insert into shells, while those remaining in their shells were more likely to feed.

Regression results indicated shell aperture width could be used to determine the appropriate shell size offered hermit crabs based on crab weight. Our results confirm those of Vance (1972) who found that for *Pagurus granosimanus*, hermit crab weight and shell width provided the best fit linear regression.

Although shells were contacted first more often than food in all four treatments, the difference was not significant. There was, however, a significant difference between initial contact time of shells and food in group C. Control hermit crabs made initial contact with shells significantly faster than with food.

Reese (1963) found that shell-less *P. samuelis* was visually attracted to shells that contrasted in color with the background. Although group C crabs were not shell-less in the current study, they could have oriented to the object that provided the greatest visual contrast for reasons other than shell acquisition.

There was a significant difference among treatments in the number of times objects were contacted. Control hermit crabs made significantly more contacts with objects than hermit crabs removed from their shells (S and StS). Having access to shells and food prior to testing likely lowered the motivation of control hermit crabs to feed or switch shells. Since they were not seeking a specific resource, group C crabs investigated each object with repeated contacts as they moved around the arena. In contrast, we suggest that groups S and StS made significantly fewer contacts because they had stronger motivation to acquire a resource at initial contact.

Hazlett (1996) found a correlation between hermit crab shell-fit deficit and shell grasping, with crabs in ill-fitting shells more likely to hang on to a shell. In our study, shell-less crabs made only one contact with the shell while shelled crabs made 1.6 ± 0.35 (St) and 2.45 ± 0.52 (C) contacts and did not hang on to the shell. Elwood (1995) showed that if the disparity between a current shell and a newly encountered shell was great, crabs made a decision quickly to accept or reject the shell. Since shelled hermit crabs in our study had access to plenty of shells prior to testing it is unlikely they were experiencing shell-fit deficit, and hence had little motivation to switch shells.

Even though starved hermit crabs (St and StS) had lower mean feeding times than group C, the difference was not significant. In addition, mean time to insert into shells was not different between shell-less crabs that acquired a shell (100 % of group S and 77.5 % of group StS) and shelled crabs that switched shells (5.0 % of group C and 8.0 % of group St). Taken together with the differences among treatments in the number of contacts with objects, this implies that increased motivation to acquire food or shells does not necessarily enable hermit crabs to find resources faster, but rather to make the decision to acquire food or shells upon first contact. This conclusion is supported by evidence that hermit crabs in group S generally inserted into the shell upon first contact, but only half of the group made any contact with food. Individual variance in locomotion rates during testing likely masked any differences among treatments in time to initial contact or behavior, if they exist.

For those treatments in which hermit crabs remained in their shells (C and St), most chose to feed and few switched shells. Hazlett (1996) observed behavior of the hermit crab, *Clibanarius vittatus*, in an 18 cm circular arena in response to food odor at 1, 4, and 7 days post-feeding while occupying inadequate shells. He found hermit crabs responded to stimuli in an apparent order of importance, such that as motivation from hunger increased, motivation to switch shells decreased; implying that as hunger increases, finding food becomes a higher priority than finding an adequate shell for *C. vittatus* (Hazlett, 1996). In the current study, hermit crabs in the C and St groups were given extra shells from which to choose, thus shell-fit was unlikely to be a motivating factor.

Since control crabs (C) had access to both food and shells prior to testing, we expected group C to exhibit equal amounts of feeding and shell-switching behavior. However, switching shells could be considered a 'risky' behavior due to the increased possibility of predation or conspecific shell-fights (Elwood & Neil, 1992). Gherardi (2006) found that hermit crabs in low-quality shells are more motivated to fight and take risks than crabs in better-fitting shells. In the current study, group C may have chosen feeding over shell-switching because crabs were not motivated by deprivation to choose the high-risk behavior.

Behavior exhibited by hermit crabs in groups C and St were unaffected by whether they had been fed or starved, respectively, prior to testing. Although feeding duration was not specifically measured, crabs in the St group continued to feed until separated from the food, while group C hermit crabs generally fed briefly then walked away.

For treatments in which hermit crabs were removed from shells, all of group S and the majority of group StS chose to insert into shells. While StS hermit crabs could have exhibited equal amounts of feeding and shell insertion, as both needs were present, significantly more chose shells than food. Taken together with the results of the C and St groups, we suggest that shell-lessness is a stronger motivator than hunger. In agreement with our conclusion, Reese (1963) found that motivation for gaining a shell in *Pagurus samuelis* was highest in shell-less hermit crabs, medium in crabs that occupied non-preferred shell species, and lowest in hermit crabs occupying preferred shell species, as measured by hermit crab activity level and tendency to explore pebbles and

aperture-sealed shells. The results of the current study concur, in that shell-less

hermit crabs (S) had the highest motivation to acquire a shell, while crabs with

competing motivations (hunger and shell-lessness, StS) exhibited a combination

of shell and food acquisition, and those in preferred-size *Tegula* shells (C and St)

had the lowest motivation to switch shells.

Since hermit crabs in suboptimal shells are at risk of desiccation,

predation, reduced growth rate, and lower reproductive success (Reese, 1969;

Vance, 1972; Angel, 2000; Yoshino*, et al.*, 2004), for hermit crabs occupying

inadequate shells, or completely lacking shells, there may be selective pressure

to recognize when a shell has the best possible fit. Elwood et al. (1998) found

that motivational state at the beginning of shell-contests differed according to the

potential gain in resource value and not according to the relative size of the

opponent; thus, it was the attacker's motivation to acquire a better shell that

influenced the decision to attack. Vance (1972) demonstrated that the adequacy

of a hermit crab's shell affects the probability of winning a shell fight, such that

the less adequate the shell, the more motivated a hermit crab is, and the more

likely to win the contest. In shell contests, defenders rarely give up shells if they

would not profit by the exchange, indicating that possessing an optimal shell

motivates hermit crabs to incur the energetic costs of keeping it (Hazlett, 1981).

Some studies have linked internal factors, such as blood glucose and oxygen

levels, lactate build-up, and hormone levels with hermit crab motivation to

acquire and keep adequate shells (Briffa & Elwood, 2001; Briffa & Elwood, 2002;

Briffa & Elwood, 2007).

Most behavioral models incorporate some degree of hierarchy, where the hierarchical interaction may be all-or-nothing or an increase/decrease of one behavior by another input (Hazlett, 1996). Stimuli, motivation, and experience may all influence behavior patterns. In the current study, evidence suggests that hunger and shell-lessness are motivations that stimulate "all-or-nothing" responses. When deprived of a shell, *P. samuelis* sought an appropriate shell at the expense of acquiring food. When shell security was not an issue, acquiring food took priority. This could be explained by prioritizing predator avoidance above other behaviors. When the shell is adequate, the risk of exposure to predators during a shell exchange may prevent hermit crabs from switching shells, as was seen in group C. When a hermit crab is motivated to both feed and acquire a shell, finding a shell takes priority.

In rocky intertidal environments, resources such as food and shells are likely to be ephemeral. Hermit crabs that are motivated to seek and acquire necessary resources have an advantage over those that are distracted by multiple objects in their environment. For shell-less hermit crabs, the need to find a shell takes priority over acquiring food, while hermit crabs in adequate shells prefer not to risk switching shells even if one is encountered. When the risk of predation or exposure means imminent death, the motivation to seek shelter can outweigh the motivation to acquire food.

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Figure Legends

Figure 1. Linear regression showing the relationship between hermit crab body weight and the preferred shell aperture width. Aperture width = 0.22 + 0.18 × Body Weight, $r^2 = 0.76$.

Figure 2. The mean time to initial contact with object (food or shell) based on treatment. Control = C, Shell-less = S, Starved = St, Shell-less and Starved = StS, * = significant differences ($p < 0.01$) between objects.

Figure 3. The mean number of contacts with objects (food or shell) based on treatment. Control = C, Shell-less = S, Starved = St, Shell-less and Starved = StS. Data represented as means $\pm$ 1 SE. Significant differences ($p < 0.001$) between treatments are indicated by the letters a and b, and between objects as *.

Figure 4. The mean time to initiate behavior based on object (food or shell) and treatment. Control = C, Shell-less = S, Starved = St, Shell-less and Starved = StS. Data represented as means $\pm$ 1 SE.

Figure 5. Behavior exhibited based on treatment during 15 minute test sessions, $p<0.001$. Control = C, Shell-less = S, Starved = St, Shell-less and Starved = StS.

Table 1. Description of the factorial treatment arrangements used to test hermit crab motivation to acquire shell and food resources.

	Fed shrimp to satiation	Starved 8-15 days
Given extra shells prior to test, Left in shell during test	Control (C)	Starved (St)
No extra shells prior to test, Removed from shell prior to test	Shell-less (S)	Starved and Shell-less (StS)

Table 2. The number of hermit crabs that first made contact with either food or shells based on treatment, p > 0.05.

			Treatment		
Object	C	St	S	StS	*Total*
Shell	27	27	25	25	104
Food	13	13	15	15	56

C, control; St, starved; S, shell-less; StS, starved and shell-less.

Table 3. The number of hermit crabs that decided to insert into shells, feed, or take no action during 15 minute sessions based on treatment.

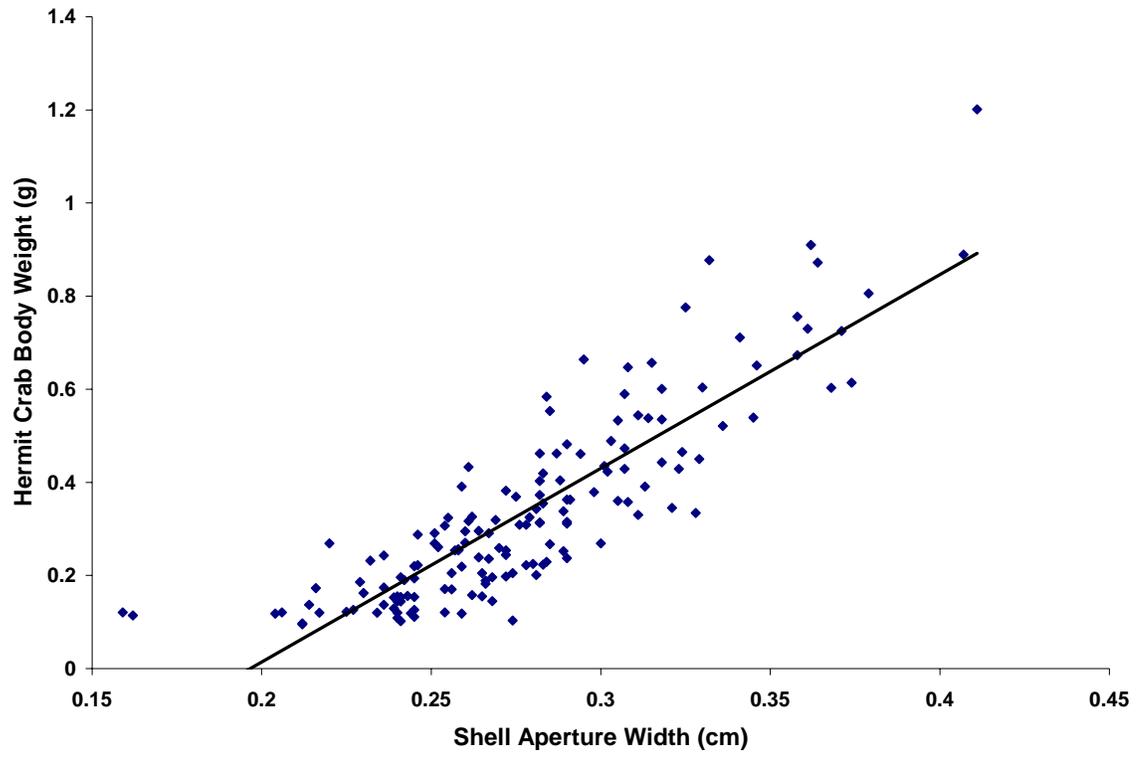|			Treatment		
Decision	C	St	S	StS	*Total*
Insert into shell	2	3	40	31	76
Feed	33	34	0	7	74
Neither	5	3	0	2	10

C, control; St, starved; S, shell-less; StS, starved and shell-less.
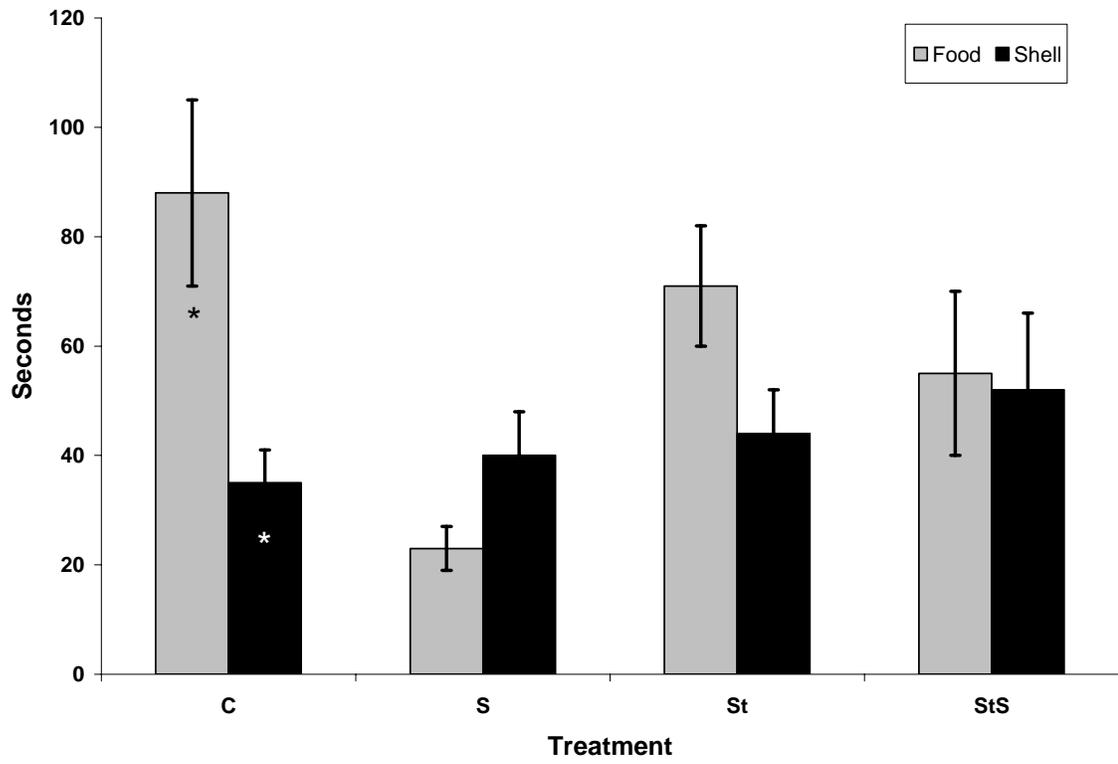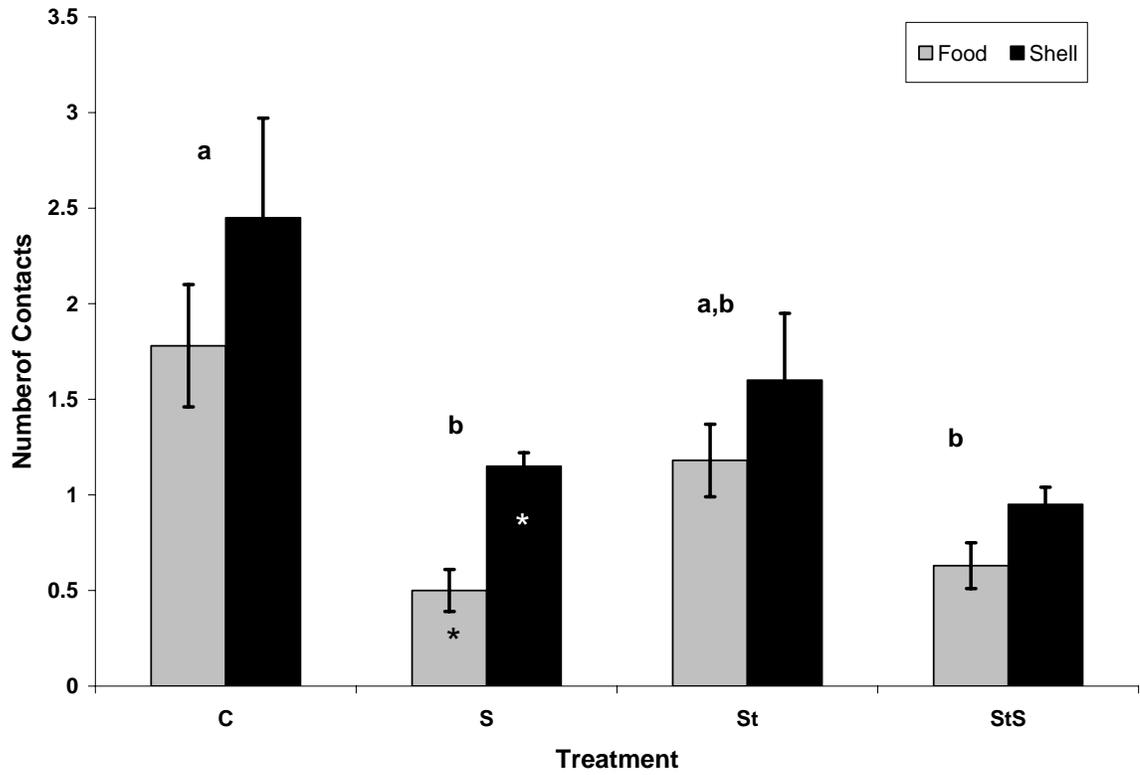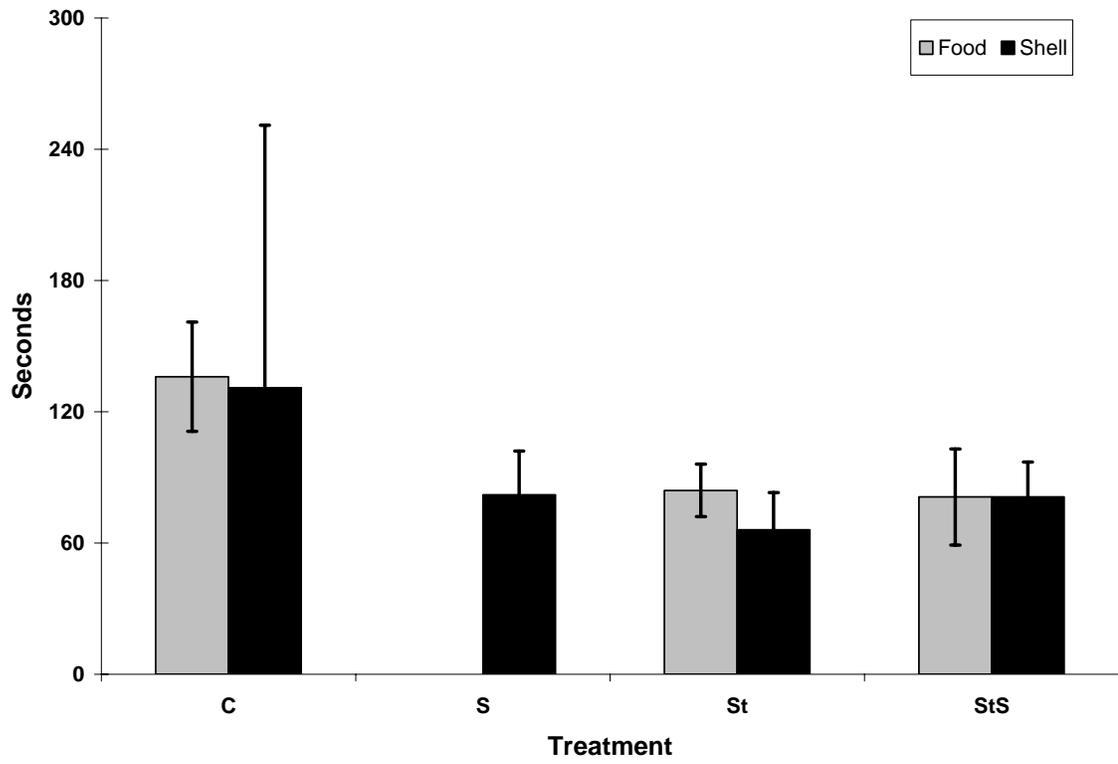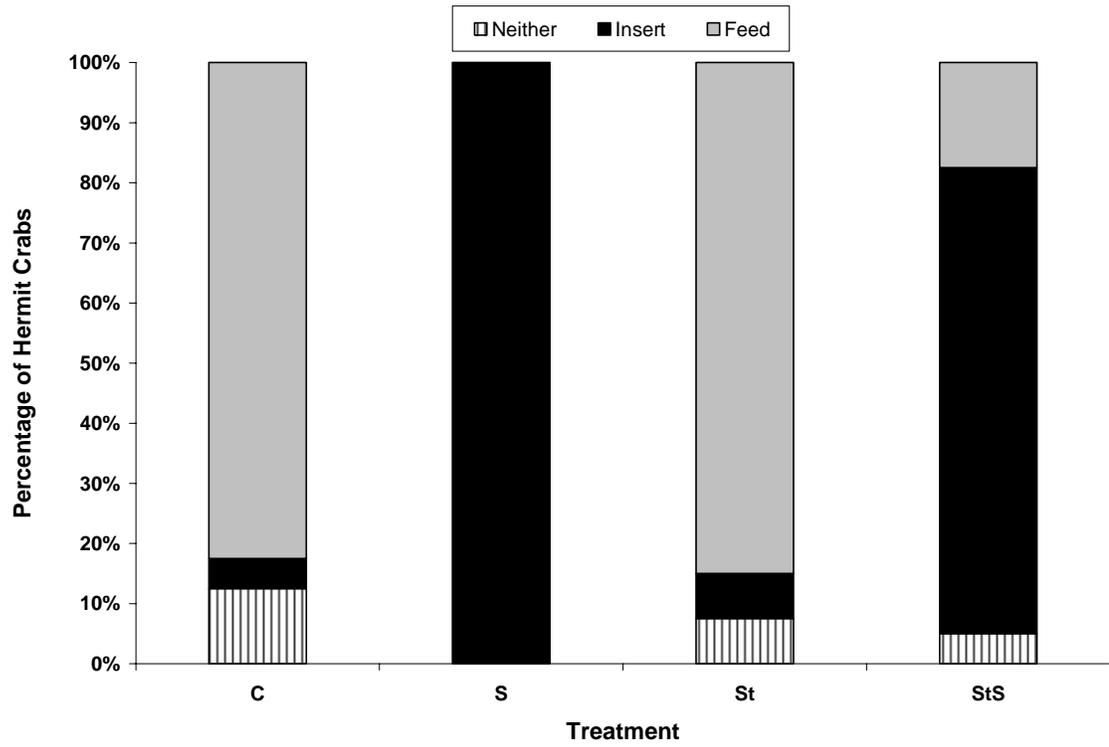
Figure 1

Figure 2

Figure 3

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Figure 4

Figure 5

CHAPTER IV

Shell and Food Acquisition Behaviors: Evidence
For Contextual Decision Hierarchies in Hermit Crabs

Wendy L. Billock and Stephen G. Dunbar

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'. In the shell acquisition
experiment, treatments that included tactile cues elicited significantly shorter
decision times (8.5 - 117.1 seconds), than treatments without tactile cues (294.5
- 765.2 seconds). In contrast to the shell acquisition experiment, we found that in
the food acquisition experiment, treatments that included chemical cues elicited
significantly shorter decision times (78.4 - 450.5 seconds), than those without
chemical cues (570.0 - 778.1 seconds). Even though 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.

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. 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.

Although one type of cue may be enough to elicit a behavioral response, a second stimulus may alter, enhance, or even replace the first cue. In the wolf spider, *Schizocosa ocreata*, visual cues were primary during foraging, but vibratory cues significantly enhanced foraging effectiveness (Persons & Uetz, 1996). In the tadpoles, *Rana lessonae* and *R. esculenta*, chemical cues were most significant in directing anti-predator behavior, but tactile cues increased the response (Stauffer & Semlitsch, 1993).

There is evidence that behavioral cues are arranged hierarchically, and 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 & 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; Rebach, 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. In addition, Billock and Dunbar (submitted) 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. 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 degree decision-making changes when the available information is altered.

Methods

Animal Collection & Maintenance

The blue-band hermit crab, *Pagurus samuelis* (Stimpson), and the black turban snail, *Tegula funebralis* (A. Adams)*,* 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 ± 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 four to seven 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 & Dunbar, submitted).

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. 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" 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 the *Tegula* food target was rinsed in seawater and redipped in wax.

Shell Acquisition

Hermit crabs were tested in a circular arena with a *T. funebralis* shell and four decoy objects: a black rubber stopper; a smooth pebble; a round piece of glass; and a small, flat piece of bivalve shell. During test sessions, visual, chemical, and tactile cues of shell availability were presented in a factorial manner (see Table 1): no cues, control (Con); 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 sunlight bulb. For non-visual treatments, the arena was dark, yet hermit crab movement could easily be viewed via the infrared camera. For chemical treatments, seawater was infused with odor of recently killed *T. funebralis*. The snail was placed in a freezer for one hour 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 hour, 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. 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 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 W × 2 cm L × 1.5 cm H) 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 and number of contacts with the shell. We also recorded the total time elapsed before insertion into the shell. A maximum of 15 minutes per session was allotted. Hermit crabs that never made initial contact with the shell scored 15 minutes for 'Initial Contact Time'. If the hermit crab never inserted into the shell, the 'Decision Time' was scored as 15 minutes.

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. 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 hours. Prior to testing, the snail was

thawed and the operculum removed.   For chemical treatments, the foot muscle

of a *T. funebralis* was left exposed, and for the non-chemical treatments the shell

aperture was sealed with wax. The arena was filled with 550 ml 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 wax. 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).

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.

Results

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 (χ^2 = 8.84, df = 7, p = 0.264).

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 η^2 = 0.454, see Figure 1). Results of Bonferroni pair-wise comparisons between treatments are displayed in Table 2. 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 Con, 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 η^2 = 0.580, see Figure 2). Results of Bonferroni pair-wise comparisons are shown in Table 3. 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 Con in decision time; however, when combined in the VC treatment, these cues elicited a significantly shorter decision time.

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.

A Kruskal-Wallis analysis of initial contact time revealed no significant differences among treatments (χ^2 = 12.11, df = 7, p = 0.097).

The mean number of contacts with the shell was significantly different among treatments (χ^2 = 53.74, df = 7, p < 0.001, see Figure 3). The results of Bonferroni pair-wise comparisons among treatments are displayed in Table 4. 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 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 wax. In Figure 4 it can be seen that the mean decision time was significantly different among treatments ($F_{7,245}$ = 35.06, p < 0.001, partial η^2 = 0.478). Results of post-

hoc Bonferroni pair-wise comparisons among treatments are displayed in Table

5. Treatments that included the chemical cue (C, VC, CT, and VCT) had the

lowest mean decision times. There was no significant difference in the mean

decision time among C, VC, and CT. The VCT treatment had a significantly

lower decision time than any of the other treatments. There was no significant

difference between Con, V, C, T, and VT.

Discussion

Shell Acquisition

In the hermit crab, *Pagurus 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

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.

Mesce (1993) found that *Pagurus samuelis* would find and inhabit a shell within

11 seconds under natural light, but required 190 seconds 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, 1993). 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. We conclude 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 be readily inhabited. It is likely that *P. samuelis* is detecting calcium on the surface of the shell. Mesce (1982) found that both *P. hirsutiusculus* 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. 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 (Con, 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 antennae ablation. In addition some species, *P. longicarpus* (Pechenik & Lewis, 2000) and *P. hirsutiusculus* (Mesce, 1993), 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.

Alone, the 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. However, when combined these cues significantly lowered mean decision time. While both Reese (1963) and Mesce (1993) 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, 1996; Rittschof & Hazlett, 1997; Gherardi & Atema, 2005), as signals of shell availability, increase hermit crab attraction to shells. In the current study, visual and chemical cues could be used to acquire shells, but the time to insertion in the VC treatment was significantly increased compared to treatments with the tactile cue.

Food Acquisition

In the context of foraging, *Pagurus samuelis* was significantly affected by which stimuli were presented. Chemical cues had a stronger effect on feeding behavior than visual or chemical 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 & 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 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, 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 & Atema,

2005); predator avoidance (Hazlett, 1996; Rittschof & Hazlett, 1997); individual recognition (Gherardi, *et al.*, 2005); and foraging (Hazlett, 1996; Rittschof & Hazlett, 1997; Morton & 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. Rock crabs may be more motivated to seek dead or injured prey, and therefore have a stronger reaction to chemical cues from mussel extract than they do to live mussel odor.

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 10 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. 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 Figures 1 and 3). In addition, the mean decision time was longer in the food acquisition context than in the shell acquisition experiment in every treatment except groups C and T (compare Figures 2 and 4). In another study, Billock and Dunbar (submitted), suggested that being shell-less may be a greater motivating context than being hungry.

Contextual Decision Hierarchies

In this investigation, 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. In the current study, hermit crabs utilized tactile over chemical and visual cues when searching for shells. In contrast, when searching for 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. We define 'Contextual Decision Hierarchies' (CDH) as the relative weighting of external information based on internal and external context. 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.

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 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 examination 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. We found that when locating a shell, *P. samuelis* had the strongest response to the primary cue of tactile information, yet in its absence, the secondary VC cue could be utilized to acquire shells. 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 & Semlitsch, 1993; Persons & Uetz, 1996).

The trigger to utilize a specific CDH may come from either the internal context (motivation) or the external context (environment). Motivation, such as deprivation of food or shells, focuses hermit crab attention on the needed resource and initiates behavior (Billock & Dunbar, submitted). 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, *Pagurus 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 & Atema, 2005). Once an internal or external context initiates a behavior, the CDH would enable the animal to prioritize information during the completion of that behavior.

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, *Uca 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 180º 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. For an animal living in the intertidal zone with consistent access to celestial cues, sun position would be the most reliable cue to use for orientation. Slope and landscape cues may be used to reinforce the celestial cues, or could be used as backup cues when the sun is obscured during cloudy days. Chiussi & 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. 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 based on the information available at a specific time or location, based on ecological and internal contexts. As the external

context changes, CDHs allow animals to adjust their attention to alternate cues and still achieve their goals.

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Table 1

Factorial treatment organization for Shell Acquisition 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 supplied by the odor that emanated from the *T. funebralis* placed in the arena. Symbols: Con = Control; 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)	Aperture (Food)
Con	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

Table 2

P values of Bonferroni pair-wise treatment comparisons based on the number of

contacts with the shell in the Shell Acquisition experiment.   Symbols: Con =

Control; V = Visual; T = Tactile; C = Chemical; VT = Visual + Tactile; VC = Visual

+ Chemical; CT = Chemical + Tactile; VCT = Visual, Chemical and Tactile; NS =

not significant; * = p < 0.001.

Stimuli	Con	V	T	C	VT	VC	CT	VCT
Con	-							
V	NS	-						
T	0.001	0.001	-					
C	NS	NS	0.039	-				
VT	0.001	*	NS	0.020	-			
VC	NS	NS	NS	NS	NS	-		
CT	0.001	*	NS	0.022	NS	NS	-	
VCT	*	*	NS	0.015	NS	NS	NS	-

Table 3

P values of Bonferroni pair-wise treatment comparisons based on decision time in the Shell Acquisition experiment.   Symbols: Con = Control; V = Visual; T = Tactile; C = Chemical; VT = Visual + Tactile; VC = Visual + Chemical; CT = Chemical + Tactile; VCT = Visual, Chemical and Tactile; NS = not significant; * = p < 0.001.

Stimuli	Con	V	T	C	VT	VC	CT	VCT
Con	-							
V	NS	-						
T	*	*	-					
C	NS	NS	*	-				
VT	*	*	NS	*	-			
VC	*	0.018	0.003	0.025	*	-		
CT	*	*	NS	*	NS	*	-	
VCT	*	*	0.026	*	0.002	*	.003	-

Table 4

P values of Bonferroni pair-wise treatment comparisons based on the number of contacts with the shell in the Food Acquisition experiment.   Symbols: Con = Control; V = Visual; T = Tactile; C = Chemical; VT = Visual + Tactile; VC = Visual + Chemical; CT = Chemical + Tactile; VCT = Visual, Chemical and Tactile; NS = not significant; * = p < 0.001.

Stimuli	Con	V	T	C	VT	VC	CT	VCT
Con	-							
V	NS	-						
T	NS	NS	-					
C	NS	NS	NS	-				
VT	NS	NS	NS	NS	-			
VC	NS	NS	NS	NS	NS	-		
CT	NS	0.004	NS	NS	0.029	NS	-	
VCT	*	*	*	NS	*	NS	NS	-

Table 5

P values of Bonferroni pair-wise treatment comparisons based on decision time in the Food Acquisition experiment. Symbols: Con = Control; V = Visual; T = Tactile; C = Chemical; VT = Visual + Tactile; VC = Visual + Chemical; CT = Chemical + Tactile; VCT = Visual, Chemical and Tactile; NS = not significant; * = p < 0.001.

Stimuli	Con	V	T	C	VT	VC	CT	VCT
Con	-							
V	NS	-						
T	NS	NS	-					
C	NS	NS	NS	-				
VT	NS	NS	NS	0.017	-			
VC	*	*	0.001	NS	*	-		
CT	*	*	*	NS	*	NS	-	
VCT	*	*	*	*	*	*	.001	-

Figure 1. 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 show mean $\pm$ 1.0 SE. The lower the number of contacts the faster the shell recognition. Strength of treatment on shell acquisition behavior: Con = V = C $\leq$ VC $\leq$ T = VT = CT = VCT.

Figure 2. The mean decision time during Shell Acquisition treatments. The maximum time per session was 900 seconds. Treatments with the same letter represent those with no significant differences among them. Error bars show mean $\pm$ 1.0 SE. The lower the decision time the faster the shell recognition. Strength of treatment on shell acquisition behavior: Con = V = C < VC < T = VT = CT < VCT.

Figure 3. 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 show mean $\pm$ 1.0 SE. The lower the number of contacts the faster the shell recognition. Strength of treatment on food acquisition behavior: Con = V = T = VT $\leq$ C = VC $\leq$ CT = VCT.

Figure 4. The mean decision time during Food Acquisition treatments. Maximum time per session was 900 seconds. Treatments with the same letter represent those with no significant differences among them. Error bars show mean $\pm$ 1.0 SE. The lower the decision time the faster the shell recognition. Strength of treatment on food acquisition behavior: Con = V = T = VT $\leq$ C $\leq$ VC = CT < VCT.
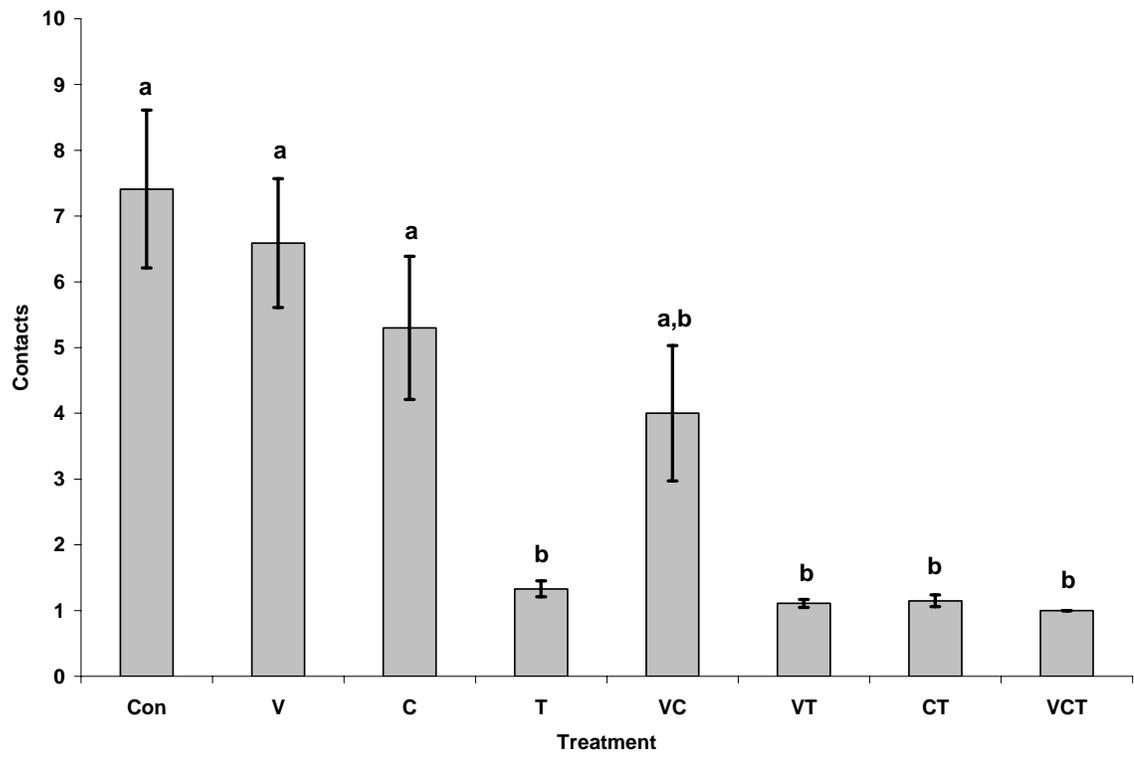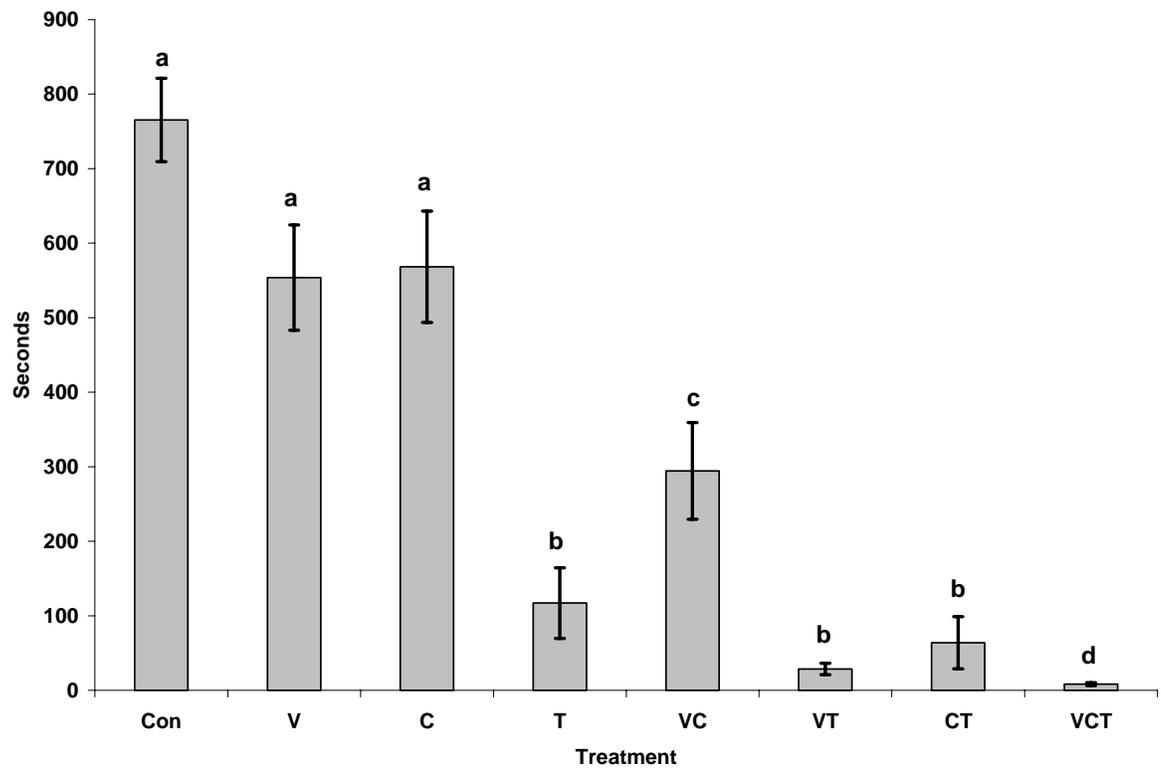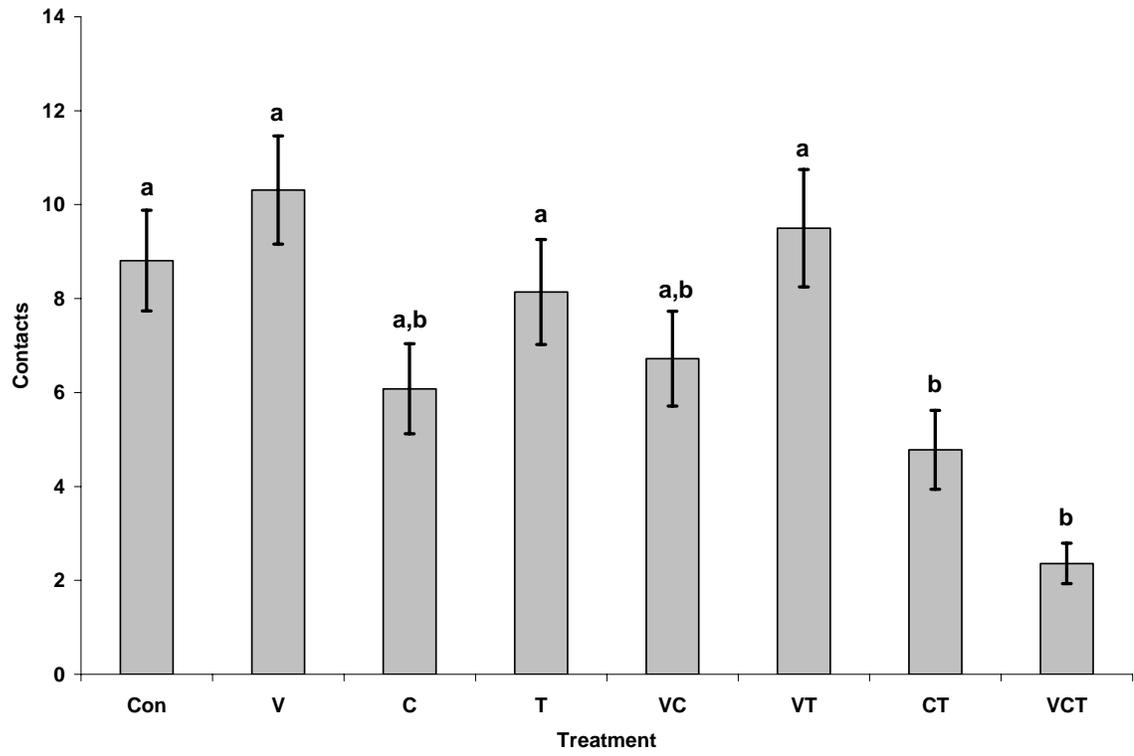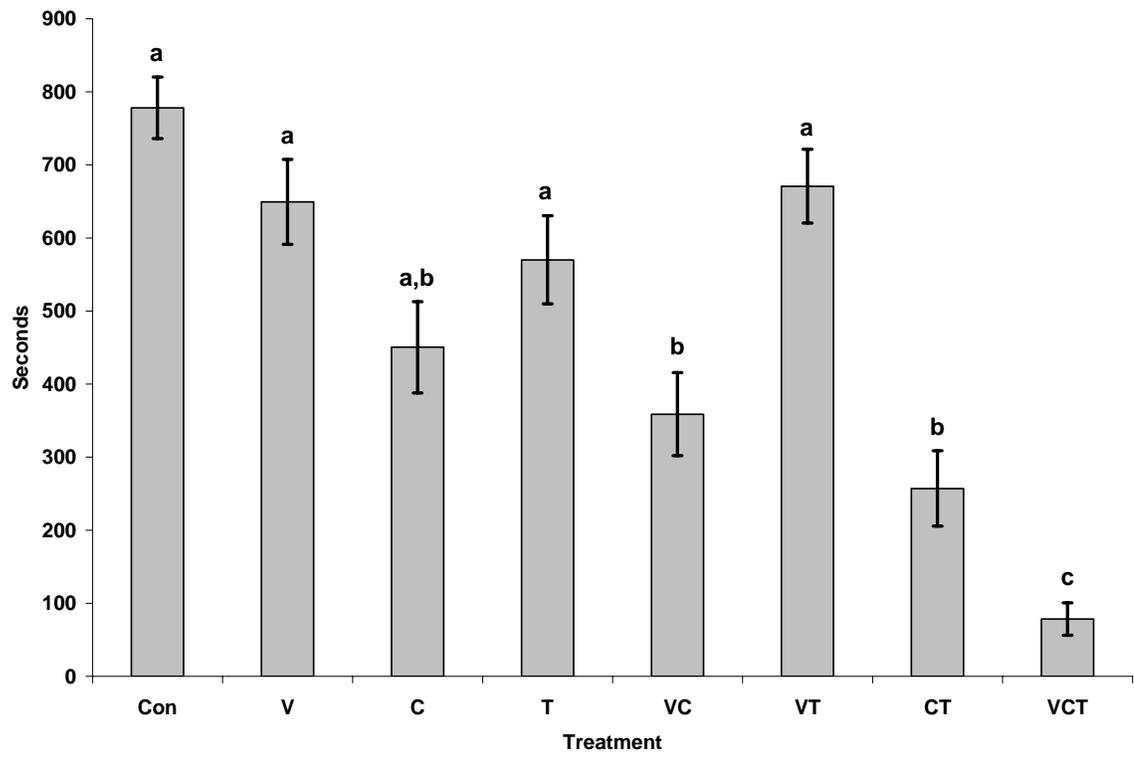
Figure 1

Figure 2

Figure 3

Figure 4

CHAPTER V

Influence of sensory cues on predator avoidance behavior
in the hermit crab, *Pagurus samuelis*.

Wendy L. Billock and Stephen G. Dunbar

Abstract

This study investigated the anti-predator behavior of the hermit crab, *Pagurus samuelis*, when exposed to various cues of the predator, *Pachygrapsus crassipes*. Visual, chemical, and tactile cues were presented in a factorial manner to determine if any sensory modality had a greater influence on behavior than others. When visual and tactile cues were available, hermit crabs removed from their shells made 43.1 – 62.9 % fewer contacts with the crab/model crab than control hermit crabs. When visual and chemical cues were present, shell-less hermit crabs made contact with empty shells 40.5 – 69.5 % faster and inserted into shells 53.7 – 72.2 % faster than control hermit crabs. For the hermit crab, *Pagurus samuelis*, visual and tactile cues appear to reduce predator encounters, while visual and chemical cues enable them to find shells. We propose that sensory modalities in *P. samuelis* are arranged in a Contextual Decision Hierarchy during anti-predatory behavior, such that visual cues are primary while tactile and chemical cues are secondary.

Introduction

The speed at which an animal detects a potential predator and takes appropriate anti-predator action may determine individual survival. Thus, accurate perception of enemies and appropriate responses to predator cues are of adaptive significance. However, defensive responses to predator cues or conspecific alarm cues are maladaptive if the threat is not real (Dicke & Grostal, 2001). Prey organisms use a variety of techniques to avoid predation. Finding adequate shelter is one such anti-predator measure. Small marine invertebrates are particularly vulnerable to predation when outside of their protective shelters.

For many hermit crab species, shelters usually consist of gastropod shells. While withdrawing into shells is a common hermit crab anti-predator behavior (Vance, 1972; Angel, 2000; Mima, *et al.*, 2003), other behaviors can also be utilized: dropping off rocks to crevices below; aggregating with conspecifics; fleeing; and burial in sand (Rebach, 1974; Bertness, 1981; Tirelli, *et al.*, 2000). Hermit crabs are subject to predation by a wide variety of animals such as sea birds, octopi, sea stars, fish, lobsters, and brachyuran crabs (Vance, 1972; Bertness, 1981; Angel, 2000; Hazlett & Rittschof, 2000; Tirelli, *et al.*, 2000; Mima, *et al.*, 2003). Hermit crabs that have lost their shells, or are living in inadequate shells, are particularly vulnerable to predation (Reese, 1969; Vance, 1972; Angel, 2000). It is at this point of increased vulnerability that they should be most responsive to cues of predation risk and shell availability.

Studies of hermit crab predation risk are usually focused on shell-fit parameters (Angel, 2000; Gherardi & Atema, 2005) or shell strength and crush-

resistance (Vance, 1972; Bertness, 1981;1982; Garcia & Mantelatto, 2001; Gilchrist, 2003; Mima, *et al.*, 2003). Other crustacean studies have looked at the latency to flee from a predator, or "startle response", in relation to either the animal's ability to detect the predator (Hemmi, 2005b;a), or the animal's perceived risk (Elwood, 1995; Elwood, *et al.*, 1998; Hazlett & Rittschof, 2000). While studies of hermit crab responses to chemical cues (Rittschof, *et al.*, 1992; Scarratt & Godin, 1992; Hazlett, 1997; Mima, *et al.*, 2003), and visual cues (Hazlett, 1982; Mesce, 1993; Diaz, *et al.*, 1995) are abundant, few studies have examined the effect of visual, chemical, and tactile cues on hermit crab anti-predatory behavior.

This study investigated changes in shell acquisition behavior of the hermit crab, *Pagurus samuelis* (Stimpson), when removed from its shell and presented with various predator cues. Visual, chemical, and tactile predator cues were presented in a factorial manner to determine if any sensory modality had a greater influence on shell-acquisition than others. While hermit crabs are known to perceive all three types of information, the relative influence of each stimulus on anti-predatory behavior is unknown.

Methods

Animal Maintenance & Materials

The striped shore crab, *Pachygrapsus crassipes* (Randall), was selected as the predator species because it lives sympatrically with *Pagurus samuelis*,

and because preliminary laboratory trials indicated that *P. crassipes* would readily kill and eat *P. samuelis* removed from its shell.

The hermit crab, *Pagurus samuelis*, and the crab, *Pachygrapsus crassipes,* were collected from Little Corona del Mar, Newport Beach, California (33 35' 21" N, 117 52' 05" W) in April and June, 2007. Hermit crabs were maintained in separate 5 cm D × 7 cm H polyvinylchloride (PVC) cylinders. Animals were maintained at $24 \pm 1°$ C with ambient light and fed Crab & Lobster Bites (HBH Pet Products, Springville, Utah) two times per week. Prior to testing, each hermit crab was measured for its wet weight with and without its shell, shield length, and the aperture width and length of the occupied shell. This information was used to select appropriately sized shells for use during test sessions as done in previous studies (Billock & Dunbar, submitted-b;a).

All experiments were conducted in a room with no external light source; however, we used a green light near the video monitor to take notes. A black curtain surrounded the arena to prevent any room light from entering the test arena. The test arena was a 21.5 cm diameter acrylic cylinder covered with white Mylar to make it opaque. All hermit crab movements were observed through a video monitor attached to a Nightview digital night vision camera (Weaver Optics, Meade Instruments Corporation, California) with the infrared illuminator set at the lowest setting. The infrared camera was used for both dark and light observations.

Experimental Procedure

Hermit crabs were divided randomly into seven groups (n = 8 per group) and each individual was randomly tested in all eight treatments. Responding to a predator is a basic behavior; there was no a priori reason to suspect that male and female hermit crabs might differ in their responses. Reese (1962) found no significant difference between sexes in *P. samuelis* shell selection behavior when removed from their shells.

Visual, chemical, and tactile predator cues were presented in a factorial manner (see Table 1): no cues, control (Con); visual (V); chemical (C); tactile (T); visual-chemical (VC); visual-tactile (VT); chemical-tactile (CT); and visual-chemical-tactile (VCT). During the visual treatments, light was provided by an artificial sunlight bulb. For non-visual treatments, the arena was left dark, yet we could easily view hermit crab movement via the infrared camera. All test sessions were conducted with seawater from *Pachygrapsus* holding tanks so that predator odor would be equivalent for each test whether it included a live or model crab. Non-chemical treatments used 500 ml seawater from *Pachygrapsus* tanks, and chemical treatments used 500 ml of conspecific odor infused seawater. Conspecific odor infused seawater was produced by freezing hermit crabs (*P. samuelis*) weighing 0.37 ± 0.06 g, for 30 minutes, crushing in a vice, and then soaking in 4.0 L of *Pachygrapsus* tank seawater. During tactile treatments, we placed a live *P. crassipes* in the arena tethered by fishing line. The shore crab's claws were wrapped with Parafilm to prevent hermit crab injuries. During non-tactile treatments a model crab was used. The model crab

was made of plastic and was of similar size and color to the live crab. We simulated crab movement by gently agitating the model crab with a fishing line pulley system approximately every 15 seconds during test sessions.

Each hermit crab was offered an empty *Tegula funebralis* (A. Adams) shell, within ±1.25 mm of its preferred shell aperture width, as *P. samuelis* body weight can be used to predict the preferred shell aperture width (Billock & Dunbar, submitted-b). The starting position of the hermit crab, empty shell, and predator were placed equidistant from each other and 1 cm from the edge of the arena.

Hermit crabs were removed from their shells using a table vise. Each hermit crab was placed under a plastic box (2 × 2 × 1.5 cm) until the test began and the box was then gently lifted by a pulley system.   When the box was lifted, we recorded the time to first contact with the shell and time to insertion into the shell. Rapid initial contact and/or insertion times indicated hermit crabs recognized the presence of a predator and performed anti-predator behavior. We also recorded the number of contacts with both the empty shell and the crab/model. Few contacts with the shell indicate hermit crabs are motivated to find shelter, while many contacts imply hermit crabs are continuing to explore the arena without acquiring a shell. Making few contacts with the crab/model signifies a motivation to avoid the predator. A maximum of 15 minutes per session was allotted. Hermit crabs that never made initial contact with the shell were scored 15 minutes for 'Initial Contact Time', and those that did not insert into shells were scored 15 minutes for 'Insertion Time'.

Statistical Analysis

All statistical tests were completed using the Statistical Package for the Social Sciences (SPSS) 12.0 and 13.0. Kruskal-Wallis tests were used to analyze differences among treatments in the number of contacts with both the shell and crab. One-way repeated measures ANOVAs were conducted to determine differences among treatments in mean time to initial contact with the shell and mean time to insert into the shell. Results were confirmed with Kruskal-Wallis tests. Specific differences among treatments were analyzed with Bonferroni post-hoc tests if the main effect was found to be significant.

Results

Of the 56 test hermit crabs, eight animals died before completing all eight treatments resulting in a final sample size of 48 individuals.   Both initial contact times and insertion into shell times were not normally distributed, so the data were rank transformed resulting in normal distribution.

The mean number of contacts with the crab/crab model was significantly different among treatments (χ^2 = 27.199, df = 7, p < 0.001). There was no significant difference in number of crab contacts between group Con and group C (see Figure 1). In contrast, the other six treatments all induced significantly fewer contacts with the crab/crab model per session. Treatments that included a live crab (T, VT, CT, and VCT) ranged from 0.75 $\pm$ 0.12 (VCT) to 0.96 $\pm$ 0.16 (T) contacts per session.

The mean time to initial contact with shells was significantly different among treatments ($F_{7,41}$ = 3.774, p = 0.003, partial η^2 = 0.392, see Figure 2). This was confirmed with a Kruskal-Wallis test (χ^2 = 22.183, df = 7, p = 0.002). The V and VC treatments induced significantly shorter initial contact times than the Con and T treatments. There was no significant difference in hermit crab initial contact time among treatments that included visual cues (V, VC, VT, and VCT).

There was no significant difference among treatments in the number of contacts with the shell before insertion (χ^2 = 10.09, df = 7, p = 0.167). The mean number of contacts with the shell ranged from 1.06 $\pm$ 0.05 (VCT) to 1.60 $\pm$ 0.21 (Tactile).

Mean time for shell-less hermit crabs to insert into shells was taken to be a measure of its predator avoidance response, where shorter times indicate stronger anti-predator responses. Differences among treatments in insertion time were significant ($F_{7,41}$ = 7.03, p < 0.001, partial η^2 = .545, see Figure 3). Groups V, VC, and VCT inserted into shells significantly faster than groups Con and T.

Discussion

Being able to detect the presence of a predator and take appropriate anti-predator actions are of vital importance to the survival of any animal. For the hermit crab, *Pagurus samuelis*, we found that visual and tactile cues reduced

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encounters with the predator, while visual and conspecific chemical cues were used to acquire shells.

The hermit crab, *Diogenes avarus*, ceased locomotion when predatory crab odor was presented (Hazlett, 1997). However, Mima*, et al.* (2003) found that the hermit crab, *Pagurus filholi,* had a shorter startle response and fled faster when predatory crab odor was presented than in plain seawater or crushed conspecific odor. The reason for this response may be that hermit crabs evaluated the potential risk based on the type of predator. When the predator type is unknown, as is the case when conspecific odor is detected, staying immobile may be the best defense; however, when the predator is a shell-crushing crab, the best anti-predator response may be to flee (Mima*, et al.,* 2003). In the current study, hermit crabs were removed from their shells, so staying immobile may not present a viable option. Since predatory crab odor was present in all treatments, hermit crabs would be expected to elicit fleeing and shell-seeking behaviors in relation to their evaluation of the visual, tactile, and conspecific odor cues that were presented.

The hermit crab, *P. samuelis*, appears to utilize visual and tactile cues to detect predators. When either visual or tactile cues were present, hermit crabs averaged only one contact with the predator but made significantly more contacts when the conspecific chemical cue was presented alone. Making more than one contact with a potential predator could be a fatal error. Hazlett and McLay (2000) found that the crab, *Heterozius rotundifrons,* was responsive to chemical alarm cues or visual predator cues only after a tactile predator cue was received. In the

current study, we also found that when chemical cues were presented with tactile cues (CT), hermit crabs were more responsive (i.e. made fewer contacts and recognized the predator faster) than when the conspecific chemical cue was presented alone (C). However, tactile cues were not needed to reinforce visual cues, as groups V and VT both made significantly fewer contacts with the predator than control hermit crabs. The difference among treatments was not based on whether it was a live crab or a model crab, since groups V and VC (model crab) were not significantly different from groups T, VT, CT, and VCT (live crab).

Group VC hermit crabs made initial contact with shells significantly faster than group Con or T. There was no significant difference in initial shell contact time among treatments that included the visual cue (V, VC, VT, and VCT) indicating that visual cues enable hermit crabs to find shells during predator avoidance.

Both Mesce (1993) and Reese (1963) concluded that *P. samuelis* can use vision to locate shells. In the current study, visual cues are likely involved not only in detecting the presence of a predator, but also in locating shelter. In addition, group C was not significantly different from groups V, VC, and VCT in shell contact time. Both Hazlett (1996) and Rittschof and Hazlett (1997) found that hermit crab locomotion increased when both conspecific blood and predator odor were presented. In the current study, dead conspecific odor likely increased hermit crab locomotion resulting in reduced initial contact time.

Hermit crabs in groups V, VC, and VCT inserted into shells significantly faster than hermit crabs in groups Con and T. Chiussi*, et al.* (2001) found that the hermit crab, *Clibanarius antillensis*, experienced increased attraction to black shapes in the presence of predator odor when removed from shells. Chemical odors emitted by predators or chemical signals from injured conspecifics commonly alert prey animals to the presence of a predator. The hermit crab, *C. vittatus*, increased shell investigation in the presence of conspecific haemolymph (Hazlett, 1995), and responded to predator odor by fleeing (Hazlett & Rittschof, 2000).

In this study we found that the chemical cue of a dead conspecific, which may strongly (although indirectly) indicate the presence of a predator, shortened both the initial contact time and insertion time compared with treatments without alarm cues. Rittschof *et al.* (1992) found that hermit crabs were attracted to crushed conspecific odor, and increased both locomotion and shell investigation behavior in response. We suggest shell-less hermit crabs in the present study responded to conspecific odor with increased attraction to shells, because dead conspecific odor can also indicate the presence of an available shell. These findings imply that visual and chemical alarm cues are used by hermit crabs to find shells and avoid predation.

Billock and Dunbar (submitted-a) proposed that hermit crabs sort information into Contextual Decision Hierarchies (CDHs). They found that for *P. samuelis*, tactile information was primary in shell-seeking behavior, but that secondary visual and chemical cues could still be used to acquire shells. In

contrast, chemical cues were primary in obtaining food, while secondary visual and tactile stimuli were reinforcing cues. For *P. samuelis,* sensory modalities also appear to be arranged in a CDH during anti-predatory behaviors, such that visual cues are primary, while tactile and chemical cues are secondary. Visual and tactile cues are used to detect the presence of a predator, while visual and chemical cues are utilized to acquire a shell.

Hazlett and McLay (2000) described the sensory hierarchy they observed in the crab, *Heterozius rotundifrons,* as "contingencies". In *H. rotundifrons*, predation risk cues such as alarm odor or over-passing shadows do not invoke anti-predatory behavior unless tactile cues are received first. Once tactile cues were received, the addition of the chemical cue of alarm odor lengthened the anti-predator behavior compared with seawater. In the absence of tactile cues, food cues were dominant over alarm cues, but when tactile cues were present, alarm odor took precedence over food cues in directing behavior (Hazlett & McLay, 2000). Stauffer and Semlitsch (1993), working with the tadpoles, *Rana lessonae* and *R. esculenta,* suggested that tactile cues provided additional information about the predator, such as direction, but were inconsequential by themselves, since it would be too costly to respond to all tactile stimuli (motion in the water) without an appropriate chemical cue signaling danger.

In the current study, tactile cues had an additive effect on predator detection, and chemical cues had an additive effect on predator avoidance, or shell-seeking behavior. We suggest that *P. samuelis* visual acuity is limited and therefore secondary cues are needed to heighten anti-predatory responses. We

agree with Stauffer and Semlitsch (1993) that it would be too costly to respond to inaccurate visual cues without confirmation of danger through secondary cues.

During certain environmental conditions, a hermit crab may have access to all visual, chemical, and tactile cues of predator presence. In other situations, such as during darkness, high sedimentation, or extreme wave action, information available to a hermit crab may be limited. In addition, although information can be perceived in all three sensory modalities, simultaneous processing of all cues could take longer than processing only one or two cues. We therefore suggest that the hermit crab, *P. samuelis*, employs an anti-predatory CDH such that visual and tactile information is used to detect predators, but visual and chemical cues are used to acquire a shell in the presence of a predator. Overall, visual cues appear to be primary in predator avoidance behaviors, while chemical and tactile cues are secondary.

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Figure 1. Mean number of contacts with a crab/model crab per session. Each letter represents treatments with no significant difference among them. Error bars show mean ± 1.0 SE. Data is interpreted as the fewer the contacts with the predator, the stronger the anti-predator response (i.e. shorter decision time).

Figure 2. The mean time to initial shell contact. The maximum time per session was 900 seconds. Each letter represents treatments with no significant difference among them. Error bars show mean ± 1.0 SE. Data is interpreted as the shorter the initial contact time, the stronger the anti-predator response (i.e. shorter decision time).

Figure 3. The mean time to hermit crab insertion into shells. The maximum time per session was 900 seconds. Each letter represents treatments with no significant difference among them. Error bars show mean ± 1.0 SE. Data is interpreted as the shorter the insertion time, the stronger the anti-predator response (i.e. shorter decision time).

Table 1

Factorial treatment organization for predator avoidance experiment. Chemical cues

supplied by either *Pachygrapsus* tank seawater (crab odor) or dead conspecific,

Pagurus samuelis, soaked in crab tank seawater (conspecific + crab odor). Symbols:

Con = Control; 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	Crab	Seawater
Con	Dark	model	crab odor
V	Full spectrum	model	crab odor
C	Dark	model	conspecific + crab odor
T	Dark	live crab	crab odor
VC	Full spectrum	model	conspecific + crab odor
VT	Full spectrum	live crab	crab odor
CT	Dark	live crab	conspecific + crab odor
VCT	Full spectrum	live crab	conspecific + crab odor

Figure 1
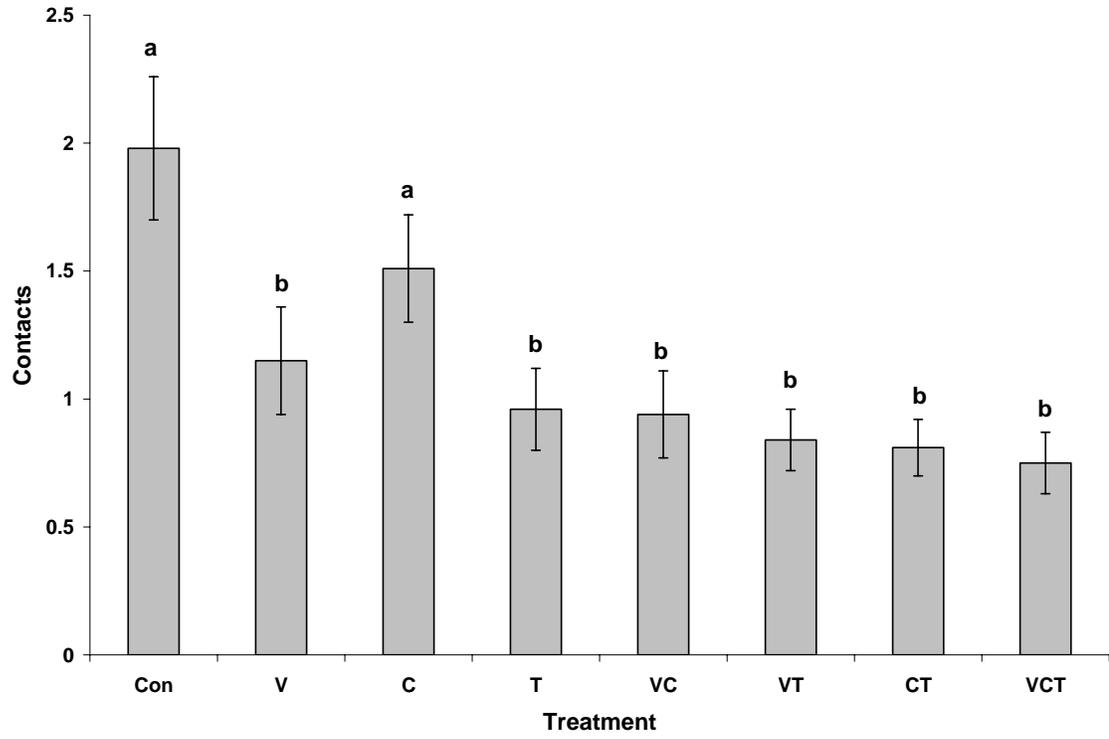
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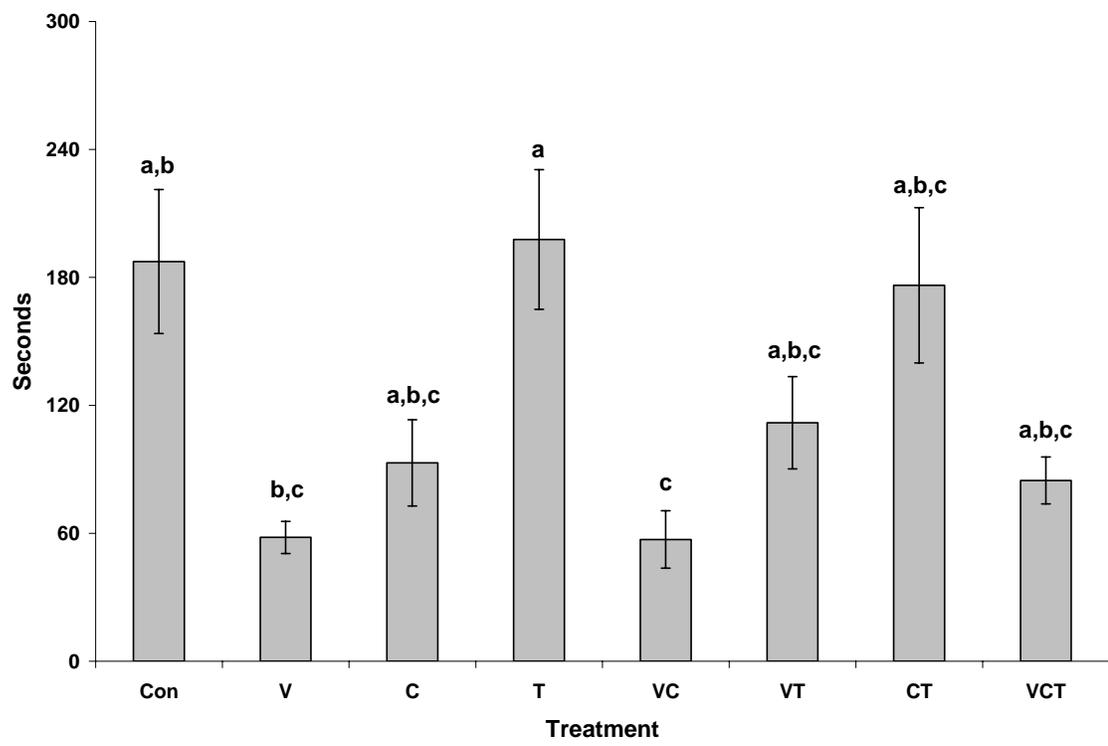
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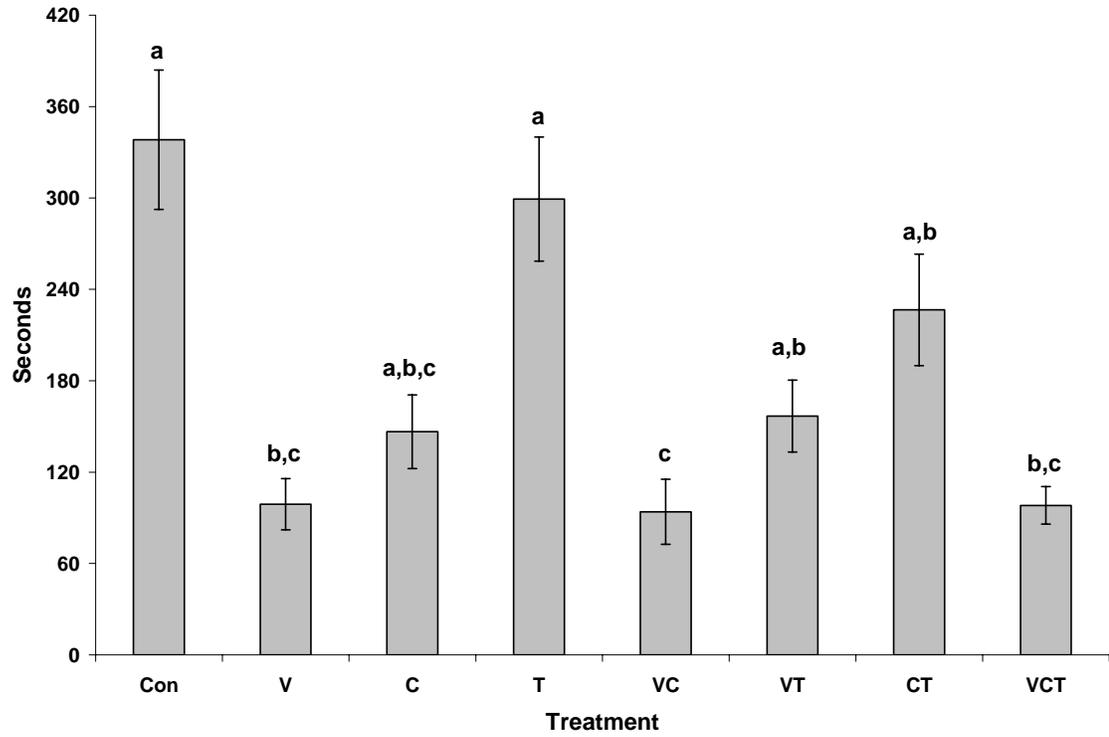
CHAPTER 6

CONCLUSIONS ON HERMIT CRAB BEHAVIOR

In this dissertation I examined how sensory information is utilized by hermit crabs in decision making. First, I confirmed that hermit crabs deprived of resources, such as shells and food, are motivated to seek the needed resource at the expense of acquiring other potential resources of which they have not been deprived. Next I explored the role of visual, chemical, and tactile cues in decision-making during three behaviors: shell acquisition; food acquisition; and predator avoidance. In light of the results from this research, I proposed a new behavior model, "Contextual Decision Hierarchies", in an effort to explain the differential use of sensory information in executing behaviors. Here, I review some of the primary conclusions of each chapter.

Chapter 2

In this review of crustacean cognition, I discussed five attributes of cognition: attention; representation; learning; solving novel problems; and contextual modulation. I then reviewed behavioral experiments that demonstrated the underlying sensory processing of visual, chemical, and tactile sensory modalities that control and modify crustacean behavior. I concluded with a discussion of a new behavior model, "Contextual Decision Hierarchies".

The five attributes of cognition allow for biologically relevant behavioral choices. Selective attention allows an animal to filter out irrelevant information

and direct its attention to a specific pattern or cue useful for decision-making (Dukas, 1998). I discussed three ways that invertebrates use representations: predator-type recognition; social recognition; and resource value recognition. Learning benefits organisms by improving functioning with experience thereby reducing the decision time of subsequent encounters with familiar situations, such as foraging. Problem solving capabilities have been demonstrated in invertebrates such as spiders and social insects, as well as some crustaceans. Contextual modulation allows animals to make appropriate decisions based upon the current situation, such as altering foraging behavior when a predator is detected.

Among crustaceans a variety of sensory receptors allows them to utilize visual, chemical, and tactile information. Most crustaceans possess compound eyes with visual capabilities ranging from simple light detection to complex color, ultraviolet, and polarized light vision. All crustaceans bear two pairs of antennae, which are the site of the majority of the animal's chemoreception. The various appendages of crustaceans can detect both chemical and tactile cues.

Visual information is used by crustaceans for: migration & orientation (Rebach, 1983; Chiussi & Diaz, 2002); foraging (Cannicci, *et al.*, 1996); recognizing predators (Chiussi, 2002; Hemmi, 2005); and finding shelter (Hazlett, 1982; Diaz, *et al.*, 1995). Chemical cues are also used for: migration & orientation (Diaz, *et al.*, 1999; Nevitt, *et al.*, 2000); foraging (Zimmer-Faust & Case, 1983; Moore & Grills, 1999; Salierno, *et al.*, 2003); recognizing predators (Chiussi, 2002; Chiussi & Diaz, 2002); and finding shelter (Orihuela, *et al.*, 1992;

Chiussi, *et al.*, 2001; Gherardi & Atema, 2005; Tricarico & Gherardi, 2006).

Tactile information can include chemosensory cues or "taste" (Dicke & Grostal, 2001), as well as mechano-sensory cues such as shape, size, texture, and weight information (Elwood & Neil, 1992:56).

I next described the way that information is prioritized into hierarchies. I defined "Sequential Decision Hierarchies" (SDHs) as the use of specific sensory cues in the execution of a series of discrete steps in a behavior. During the use of SDHs, one stimulus initiates the first behavior, another cue initiates the second behavior, and so on until the task is completed. Examples of SDHs include: jellyfish migration (Graham, *et al.*, 2001); bee orientation (Chittka, *et al.*, 1995; Fauria, *et al.*, 2004); and crustacean foraging (Derby, *et al.*, 2001). SDHs serve to focus animal attention on a specific cue or condition at each stage of a behavioral sequence, and give the flexibility to modify and correct actions at each behavioral segment.

I contrasted SDHs with the new concept of "Contextual Decision Hierarchies" which occur when various sensory modalities are ranked in order of influence on a single behavior. CDHs enable animals to direct their attention to a single sensory modality during a behavior, yet maintain the flexibility to switch to a secondary or tertiary stimulus if the primary one is unavailable or ambiguous. CDHs can provide several benefits. First, by focusing attention on a primary cue, accurate decisions can be made quickly and reliably at each occurrence. Second, by utilizing a hierarchy, secondary information from other sensory modalities can still be accessed when the primary cue is unreliable (i.e. switching

from visual to olfactory cues in the dark).   Lastly, secondary cues may act synergistically in reinforcing or modifying cues, though secondary cues may not themselves be necessary for eliciting the specific behavior. Evidence from many taxa suggest that CDHs are widespread: frogs (Stauffer & Semlitsch, 1993); spiders (Persons & Uetz, 1996); bees (Collett, *et al.*, 1997; Menzel, *et al.*, 1998; Gould, 2002); crabs (Chiussi & Diaz, 2001); and hermit crabs (Billock & Dunbar, submitted).

Chapter 3

        Both the need for shelter and the need for food can be motivations that alter animal behavior. We tested the hypothesis that the hermit crab, *Pagurus samuelis*, deprived of food (group St), shells (group S), or both (group StS) will respond differently from control hermit crabs (group C) when presented with food and shells concurrently. We measured the number of contacts made with both food and shells, and time elapsed until hermit crabs either began feeding or inserted into shells. We interpreted making few contacts and initiating behavior quickly to be an indication of short decision time and high motivation; whereas, making many contacts and having long initiation time indicated a long decision time and low motivation to acquire resources.

        Control (C) hermit crabs made 72 % more contacts with food and 53 % more contacts with shells than shell-less (S) crabs. Control hermit crabs also made 34 % more contact with food and 35 % more contacts with shells than starved and shell-less (StS) hermit crabs. ANOVA results showed significant

main effects in the number of contacts made for both objects ($F_{3,304}$ = 16.014, p < 0.001, partial η^2 = 0.09) and treatment ($F_{3,304}$ = 9.705, p < 0.001, partial η^2 = 0.05). This suggests that shell-less hermit crabs were more motivated to acquire shells than control crabs.

Treatment significantly affected the final behavior exhibited by hermit crabs (χ^2 = 114.67, df = 6, p < 0.001). Hermit crabs in the C and St groups chose to feed while crabs in the S and StS groups chose to insert into shells. It is interesting to note that hermit crabs with no deprivation (group C) chose to feed while hermit crabs deprived of both food and shells (group StS) chose to acquire shells. Switching shells could be considered a 'risky' behavior due to the increased possibility of predation or conspecific shell-fights (Elwood & Neil, 1992). Gherardi (2006) found that hermit crabs in low-quality shells are more motivated to fight and take risks than crabs in better-fitting shells. In the current study, group C may have chosen feeding over shell-switching because crabs were not motivated by deprivation to choose the high-risk behavior. Conversely, being shell-less may pose an imminent risk of injury or death, which could explain why starved and shell-less crabs (StS) chose shells over food.

Our results indicated that being shell-less was a stronger internal motivation than being starved, such that finding shelter takes priority over finding food when both are needed. In rocky intertidal environments, resources such as food and shells are likely to be ephemeral. Hermit crabs that are motivated to make appropriate decisions to acquire specific resources have an advantage over those that are distracted by numerous objects in their environment.

Chapter 4

Shell and food acquisition behaviors of the hermit crab, *Pagurus samuelis*,

were examined in response to cues of shell and food availability. During test

sessions, visual, chemical, and tactile cues of shell availability were presented in

a factorial manner: no cues, control (Con); visual (V); chemical (C); tactile (T);

visual-chemical (VC); visual-tactile (VT); chemical-tactile (CT); and visual-

chemical-tactile (VCT). We measured the number of contacts with the resource

(food or shells), time to initial contact, and time to initiate behavior. We

considered the time difference between initial contact and subsequent behavior

to be a measure of hermit crab 'decision time'.

In the shell acquisition experiment, treatments that included tactile cues

elicited a stronger response. 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 η^2 = 0.454). Hermit crabs made significantly

fewer contacts with the shell (an indication of rapid recognition of the shell)

during treatments that included the tactile cue (T, VT, CT, and VCT), than they

did in non-tactile treatments. In addition, the difference among treatments in

decision time was significant ($F_{7,182}$ = 35.93, p < 0.001, partial η^2 = 0.580).

Likewise, treatments that included the tactile cue induced significantly lower

mean decision times (an indication of rapid acceptance of the shell), than during

non-tactile treatments. Alone, the V and C treatments were not significantly

different from Con in decision time; however, when combined in the VC

treatment, these cues elicited a significantly shorter decision time. Research has

shown that *P. samuelis* (Reese, 1963; Mesce, 1993), as well as *P. longicarpus* (Pechenik & Lewis, 2000) and *P. hirsutiusculus* (Mesce, 1993) can utilize tactile cues to locate shells in the dark.

In contrast to the findings of the shell acquisition task, we found that in the food acquisition experiment the primary cue in directing foraging behavior was chemical information. The mean number of contacts with food was significantly different among treatments (χ^2 = 53.74, df = 7, p < 0.001) and hermit crabs made significantly fewer contacts with the gastropod (an indication of rapid recognition of food) when the chemical cue of gastropod odor was present than during non-chemical treatments. The mean decision time was significantly different among treatments ($F_{7,245}$ = 35.06, p < 0.001, partial η^2 = 0.478), with treatments that included the chemical cue eliciting the shortest decision times (an indication of rapid acceptance of food).

Even though primary cues elicited the shortest decision time in each of these tasks, 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 proposed that hermit crabs sort environmental information into 'Contextual Decision Hierarchies' in order to make accurate and efficient behavioral choices.

Chapter 5

This study investigated the anti-predatory behavior of the hermit crab, *Pagurus samuelis*, when exposed to various cues of the predator, *Pachygrapsus*

crassipes. Visual, chemical, and tactile cues were presented in a factorial

manner to determine if any sensory modality had a greater influence on behavior

than others.

When visual and tactile cues were available, hermit crabs removed from

their shells made 43.1 – 62.9 % fewer contacts with the crab/model crab than

control hermit crabs (χ^2 = 27.199, df = 7, p < 0.001). When either visual or tactile

cues were present, hermit crabs averaged only one contact with the predator (an

indication that they recognized the predator) but made significantly more contacts

when the conspecific chemical cue was presented alone (indicating they did not

recognize it as a predator). Making more than 1 contact with a predator would be

a fatal error. Tactile information may reinforce the primary visual cue of the

presence of a predator.

When visual and chemical cues of a predator were present, shell-less

hermit crabs made contact with empty shells 40.5 – 69.5 % faster ($F_{7,41}$ = 3.774,

p = 0.003, partial η^2 = 0.392) and inserted into shells 53.7 – 72.2 % faster than

control hermit crabs ($F_{7,41}$ = 7.03, p < 0.001, partial η^2 = .545). Groups V, VC,

and VCT inserted into shells significantly faster than groups Con and T.   Other

hermit crab species have shown increased attraction to shells or shell shaped

objects in the presence of predator or conspecific odors (Hazlett, 1995; Chiussi*,*

et al., 2001).

In this study we found that the chemical cue of a dead conspecific, which

may strongly (although indirectly) indicate the presence of a predator, shortened

both the initial contact time with shells and shell insertion time, compared with

treatments without alarm cues. Rittschof, *et al.* (1992) found that hermit crabs were attracted to crushed conspecific odor, and increased both locomotion and shell investigation behavior in response. We suggest shell-less hermit crabs in the present study responded to conspecific odor with increased attraction to shells, because dead conspecific odor can also indicate the presence of an available shell. These findings imply that visual and chemical alarm cues are used by hermit crabs to find shells and avoid predation.

For the hermit crab, *Pagurus samuelis*, visual and tactile cues appear to reduce predator encounters, while visual and chemical cues enable them to find shells. We proposed that sensory modalities in *P. samuelis* are arranged in a Contextual Decision Hierarchy during anti-predatory behavior, such that visual cues are primary while tactile and chemical cues are secondary.

Conclusion

Hermit Crabs are faced with various internal and external contexts that must be attended to such as; hunger, risk of desiccation, and risk of predation. With millions of sensory neurons, they are capable of perceiving visual, chemical, and tactile information with surprising detail and accuracy. It is unlikely that the neural processing centers in hermit crabs can process the high volume of neural receptors that may be activated simultaneously. They need a way to process information effectively and efficiently to make the best possible decisions in the least amount of time. It is likely that hermit crabs filter incoming information when searching for resources, or avoiding potential dangers. We propose that

Pagurus samuelis arranges stimuli into 'Contextual Decision Hierarchies' (CDHs) in order to streamline the information processing procedure.

Our results indicate that the three contexts of foraging, shell-seeking, and anti-predatory behavior each had a different CDH.

Shell-Seeking	Foraging	Anti-predatory
1. Tactile	1. Chemical	1. Visual
2. Visual-Chemical	2. Visual or Tactile	2. Chemical or Tactile
3. Visual or Chemical		

In addition, the results of our first experiment indicate that during multi-contextual situations, one behavior can over-ride another. For example, when hermit crabs were shell-less and starved, shell-seeking was the primary motivation; however, when hermit crabs were neither starved nor shell-less, foraging took priority over switching shells.

Contextual Decision Hierarchies may exist not only in hermit crabs, but in other invertebrates or vertebrates as well. Prioritizing sensory cues based on context means less sensory processing and hence, faster decisions. It also gives the flexibility to use alternate stimuli when the primary cue is unavailable or unreliable. Potentially, CDHs could be flexible enough to allow for behavioral plasticity across the range of a species.

Foraging, seeking shelter, and avoiding predators are common animal behaviors. They are also time-sensitive behaviors in the sense that decisions must be made rapidly and accurately to assure survival. Having the ability to focus attention on only one or two cues could increase the decision rates and

shorten response time. In principle, an animal could focus on one sensory

modality during a task, such as visually foraging, while leaving an alternate

sensory modality available for another task, such as monitoring for predator

odors. Potentially, CDHs may be utilized not only by invertebrates with limited

neural processing capabilities, but also by higher taxa that need to organize

multiple tasks and complex sensory processing.

While this dissertation is intended to answer some questions about

invertebrate cognitive responses and introduce the term Contextual Decision

Hierarchies, it also raises many more questions. Results from the motivation

experiment in Chapter 3 indicated that being shell-less was a stronger motivation

than being starved. Are other motivations arranged in a hierarchy? For

example, does foraging take precedence when hermit crabs are in sub-optimal

shells rather than shell-less? In addition, we did not measure the time spent

feeding, only the time to initiate feeding. Perhaps there are differences in

motivation to continue feeding between starved and satiated hermit crabs that we

did not test for in the first experiment.

In Chapter 4 we tested the role of visual, chemical, and tactile cues on

foraging and shell-seeking separately. Future research could look at the CDH for

starved and shell-less hermit crabs. Based on our motivation results, it is likely

that if hermit crabs are motivated to seek a shell they will use the shell-seeking

CDH rather than the foraging CDH, although a combination of CDHs could result.

In Chapter 5 we examined the sensory hierarchy of anti-predatory

behavior when the predator odor was held relatively constant but the conspecific

odor cue varied. How would the CDH change, if at all, to alternative predator cues? Do hermit crabs respond differently to various predators such as birds, crabs, and fish?

My research focused on *Pagurus samuelis* from southern California. Potentially, other populations, such as the northern range of *P. samuelis*, could use alternative CDHs that are locally relevant. Likewise, a closely related sympatric species such as *P. hirsutiusculus,* could use the same or alternative CDHs. Future work could also search for evidence of CDHs in other crustacean, invertebrate, and even vertebrate species.

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