



The scent of cannibalism: The olfactory basis of cannibalism in hermit crabs

Mark V. Tran*

Department of Zoology/Ecology, Evolutionary Biology, and Behavior Program, Michigan State University, East Lansing, MI, USA



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ABSTRACT

Animals are constantly exposed to sensory cues that provide conflicting information about their environments and must somehow rely on these sensory cues to make appropriate behavioral decisions. For cannibalistic scavengers, the odors of injured conspecifics or heterospecifics can serve as conflicting sensory cues because they could represent either the proximity of a food resource or the proximity of a predator (e.g., a recent predation event). Foraging cannibals must therefore weigh the risk–reward consequences of approaching injured conspecifics and heterospecifics. Previous research has shown that foraging cannibals respond to these conflicting cues by exhibiting caution, showing anti-predation behaviors instead of foraging behaviors. Hermit crabs are cannibalistic animals that rely heavily on olfaction to forage. Here I show for the first time that cannibalistic hermit crabs use the odors of crushed conspecifics and heterospecifics as foraging cues instead of anti-predation cues. Test animals, in general, responded to the odors of crushed conspecifics and heterospecifics with increased foraging responses instead of anti-predation responses, and readily consumed both conspecific and heterospecific animals. However, test animals showed faster approach times and longer feeding times for heterospecifics than conspecifics. These results suggest that hermit crabs are capable of discerning between the odors of conspecifics and heterospecifics, and show greater avoidance towards dead conspecifics than heterospecifics.

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1. Introduction

Cannibalism is widespread across the animal kingdom and is believed to be an adaptive foraging strategy in many ecological contexts (Fox, 1975). Although cannibalism offers nutritional benefits (Crossland et al., 2011; Mayntz and Toft, 2006; Meffe and Crump, 1987; Nagai et al., 1971), it also poses potential costs to the cannibal. One such cost is an increased risk of predation directed at the cannibal, especially for scavenging cannibals that feed on dead or injured conspecifics (hereafter referred to as CONs). Because the prey's cause of death is difficult to assess from a distance, scavenging cannibals that approach dead or injured CONs could also be approaching potential predators (Ferner et al., 2005). Thus, scavenging cannibals must either be able to accurately assess their risk of death by predation before approaching a potential food source, or prioritize feeding over the risk of predation. How foraging animals assess this risk and make the appropriate decisions is poorly understood. However, it has been predicted that animals should exhibit caution when approaching injured CONs and heterospecifics (HETs; animals of closely related, sympatric species) due to the strong selection pressures associated with risk of predation

directed at the scavenger (Ferner et al., 2005; Moir and Weissburg, 2009).

Many aquatic animals rely heavily on olfaction to mediate vital processes in their daily lives, including foraging and predator avoidance (Hazlett, 2011; Rittschof, 1992). For aquatic crustaceans, risk of injury or death by predation is often assessed based on the presence or absence of “alarm” cues processed by the olfactory system (Hazlett, 2011). These alarm cues commonly consist of odors emitted from the tissues of injured CONs or HETs that are leached into the surrounding water following predation events (Hazlett, 2011). For scavenging cannibals foraging in aquatic environments, the cues leached from CON or HET tissues into the environment following bodily damage offer conflicting signals to the cannibal because they could represent either the availability of a potential food resource or the proximity of a predator. Thus, scavenging crustacean cannibals face the dilemma of using the same olfactory cues as both foraging and alarm cues (Ferner et al., 2005; Moir and Weissburg, 2009). Recent studies on the cannibalistic blue crab (*Callinectes sapidus*) have shown that these animals respond to the odors of injured CONs in a manner more consistent with risk avoidance than foraging (Ferner et al., 2005; Moir and Weissburg, 2009). However, further research on other crustacean species is needed to determine if these responses are stereotypical of all crustaceans, or are species-specific.

Hermit crabs make excellent model systems for addressing hypotheses regarding the risk–reward consequences of cannibalism because

* Corresponding author at: Department of Zoology, Michigan State University, 288 Farm Lane Rm 203, East Lansing, MI 48824, USA. Tel.: +1 517 929 5637; fax: +1 517 432 2789. E-mail address: tranmark@msu.edu.

(1) they are generalist scavengers (Hazlett, 1981) that have been documented to exhibit cannibalistic behaviors in nature (Barnes, 1997), and (2) like most aquatic crustaceans, these animals rely heavily on olfaction to mediate their foraging behaviors (Rittschof, 1992). While recent studies (Laidre, 2010; Laidre, 2013) indicate that terrestrial hermit crabs rely heavily on visual and social cues during foraging, olfaction is regarded as the primary sensory input for environmental information in aquatic hermit crabs. Additionally, ecologically similar hermit crab species often live in close sympatry (Hazlett, 1981; Mackie and Boyer, 1977; Snyder-Conn, 1980), presenting us with potentially excellent model systems for the exploration of behavioral reactions to both CON and HET odors (Hazlett and McLay, 2005).

Hermit crab CON and HET odors can be released into the surrounding water due to (1) nearby predation events or (2) injury during resource contests (e.g., limb loss during shell fights; Bertness, 1981; Neil, 1985; Scully, 1979; Scully, 1983). The intensity of resource contents, and thus the amount of physical damage inflicted during the contests, is largely dependent on the motivation of the contestants and the value of the resource being contested for (Dowds and Elwood, 1983; Laidre, 2007). While resource contests may not escalate to physical damage every time, the frequency with which these contests occurs means that hermit crabs are routinely exposed to the odors of CONs and HETs outside of the context of predation directed at hermit crabs. Since hermit crabs are scavenging cannibals and rely heavily on shells previously occupied by CONs and HETs (Laidre, 2011), the frequent detection of CON and HET odors outside of the context of predation may have resulted in hermit crabs evolving behavioral responses to CON and HET odors associated with foraging (cannibalism) or shell acquisition. While the behavioral reactions of hermit crabs to these odors have been examined in the context of shell-resource acquisition (Rittschof and Hazlett, 1997; Small and Thacker, 1994; Tricarico et al., 2011), they have not been examined in the context of cannibalism.

Examining the behavioral responses of hermit crabs to CON and HET odors in the context of cannibalism requires the use of procedures that are specifically designed to identify and quantify foraging behaviors. Previous studies suggest that when hermit crabs are stimulated to search for shells via olfactory inputs, they exhibit behaviors associated with shell acquisition and do not show behaviors associated with foraging (Rittschof, 1980; Rittschof et al., 1992). Although the behaviors exhibited by hermit crabs in response to these olfactory cues are dependent on the motivational state of each individual animal and may change as the animal reassesses its environment, the behaviors of foraging and shell acquisition appear to be independent of each other. Thus, the identification of foraging behaviors immediately after presenting an animal with CON or HET odors should serve to indicate that the animals are foraging, rather than searching for new shells.

The objectives of this study were twofold. First, I sought to examine the behavioral responses of two sympatric hermit crab species to the odors of crushed CONs and HETs to determine whether these animals use these odors as foraging or alarm cues. Second, I sought to determine if there were differences in the crabs' willingness to approach and consume dead CONs versus dead HETs. To accomplish the first objective of this study, I exposed hermit crabs to the odors of crushed CONs and HETs and measured the strengths of the crabs' foraging reactions using an established foraging behavioral assay (Tran, 2013). To accomplish the second objective, I quantified whether there were differences in the animals' (1) willingness to approach dead CONs compared to dead HETs (measured as latency to contact time) and (2) time spent feeding on dead CONs compared to dead HETs. Because both CONs and HETs represent potentially important food resources for hermit crabs, I predicted that the hermit crabs would (1) show foraging responses instead of anti-predation behaviors when exposed to the odors of both crushed CONs and HETs, (2) consume both CON and HET tissues equally, and (3) show no difference in willingness to approach dead CONs and HETs. Additionally, since an animal's risk of being eaten generally decreases with increasing body size (Moir and

Weissburg, 2009), I predicted that cannibal body size would be positively correlated with (1) the strength of their reactions to CON and HET odors, (2) their willingness to approach dead CONs and HETs, and (3) their willingness to sustain feeding on dead CONs and HETs. It is important to note that the objective of this study was to quantify how hermit crabs respond to CON and HET odors, not to compare the strength of responses between the two test species. The two test species were used in order to determine if any trends observed were species-specific, or could be extrapolated to be considered more general behaviors of hermit crabs.

2. Materials and methods

2.1. Study system

Clibanarius digueti (Bouvier, 1898) and *Paguristes perrieri* (Bouvier, 1895) are ecologically similar, sympatric hermit crab species that coexist in the intertidal region of the Gulf of California (Ayón-Parente and Hendrickx, 2010) and have been documented to form large, mixed-species clusters (Snyder-Conn, 1980; personal observation) which likely facilitate shell switching between individuals (Gherardi and Tricarico, 2011). Because of the aggressive nature of shell contests in hermit crabs, and the potential bodily damage that accompanies such aggression, these clusters likely also facilitate cannibalistic encounters. Like most hermit crab species (Hazlett, 1981), these species are detritus and carrion scavengers. Because the two species are sympatric and of similar body sizes (Harvey, 1988), they likely share common predators, although this has not been documented. Hermit crab predators generally include fish, octopi, and birds, all of which are present in the intertidal region of the Gulf of California.

2.2. Animal housing and maintenance

Wild-caught *C. digueti* and *P. perrieri* were obtained from a commercial distributor (A & M Aquatics, Lansing, MI) and housed in mixed-species groups in 10-gallon glass aquaria containing sand substrate and aerated artificial salt water (ASW; Instant Ocean). This ASW and other ASW mentioned in this report was maintained at a specific gravity of 1.021–1.025, temperature 23–29 °C, and pH 8.2–8.4. Animals were acclimated to laboratory conditions for a minimum of 2 weeks prior to testing while being kept under a 12 h light:12 h dark cycle and fed a diet of pellet food (NewLife Spectrum) three times per week. The quantity of food provided (~2 pellets per animal) was adequate to keep the crabs in a healthy physiological state while avoiding the buildup of nitrogenous waste products emanating from uneaten food. During acclimation, aquaria were stocked with a number of empty shells of different sizes and shapes so the animals could selectively choose optimally-fitting shells.

2.3. Testing apparatus

The testing apparatus used in all experiments consisted of a 250 mL glass Erlenmeyer flask filled with 250 mL ASW and clean gravel substrate.

2.4. Behavioral reactions to the odors of crushed CONs and HETs

The three test stimuli used in these experiments were crushed CONs, crushed HETs, and plain ASW (control). ASW was chosen as the control for these experiments because (1) it has been shown to elicit no behavioral response in these species (Tran, 2013), and (2) including a stimulus that elicits no behavioral response is necessary to ensure the unbiased scoring of behavioral responses across stimuli (i.e., it prevents the observer from biasing towards high behavioral scores). One medium sized animal (shell length 2.1–2.7 cm) of each species was randomly selected from a population tank each day and used for stimulus

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