



# Behavioral reactions to novel food odors by intertidal hermit crabs



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## ABSTRACT

Novel food items represent important food resources for generalist scavengers, such as intertidal hermit crabs. For animals that rely heavily on olfaction to mediate foraging, their first encounters with novel food items come from the detection of novel food odors. Although crustaceans have been shown to possess sensory mechanisms for processing novel odors, little is known about the level of stimulus reinforcement needed to maintain behavioral responses to novel food odors upon subsequent exposures. In the context of foraging, reinforcement of a novel food odor comes from feeding on the novel food item after sensory detection of the food item. This study tested the behavioral responses of hermit crabs to a novel food odor over repeated exposures both with and without stimulus reinforcement. The results show that stimulus reinforcement is needed for the animals to maintain their baseline level of behavioral responses to the novel food odors. Animals that were allowed to feed on the novel food item after first exposure (reinforced treatment) maintained strong behavioral reactions to the novel food odor during subsequent exposures. The behavioral reactions of animals that were not allowed to feed on the novel food item after first exposure (unreinforced treatment) rapidly declined.

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## 1. Introduction

Novel food items can provide valuable food supplements to the diets of foraging animals. The consumption of novel foods can be especially important for animals facing nutritional stresses imposed by environmental conditions, such as seasonal food scarcity or intense food competition. For these reasons, the consumption of novel foods can be considered an adaptive foraging strategy as long as foragers can accurately assess the edibility of novel items. In the context of foraging, a novel food item can be operationally defined as a food item with which a forager has no prior experience or a food item for which the forager retains no learned associations despite prior experiences with the food item.

Despite the potential nutritional benefits of consuming novel foods, many animals, including birds (Greenberg, 1990), rodents (Galef et al., 1983; Galef et al., 1984), and primates (Pliner and Stallberg-White, 2000; Visalberghi et al., 2003) exhibit neophobic responses to novel foods. This neophobia towards novel foods is generally a strategy exhibited by the forager to limit the potential for food-induced illness when consuming unknown foods. The willingness to consume novel foods varies widely among species.

For many species, the willingness to ingest novel food items is dependent on environmental factors such as social facilitation. For example, Norway rats (Galef et al., 1983, 1984, 1985) rely on social cues from conspecifics that have previously consumed the novel food in order to overcome their normal neophobic responses to the food. These social cues inform the forager of the novel food's value and potential danger, and may serve to increase the consumption of novel foods.

It can be predicted that species with broad feeding niches (such as generalist scavengers or ecologically plastic species) should be more willing to consume novel foods. Indeed, links between the diversity of environmental resources used by a species and its propensity to use novel resources have been demonstrated (Greenberg, 1990). Generalist scavengers can utilize a wide array of food resources, and can gain nutritional benefits from eating novel foods encountered during foraging, especially under conditions of food scarcity or in environments with unpredictable food availability. This makes generalist scavengers an attractive model in which to test hypotheses regarding the acceptance and consumption of novel foods.

While the majority of studies on animal responses to novel foods have utilized terrestrial vertebrates, such as birds (Greenberg, 1990), rats (Galef and Osborne, 1978; Galef et al., 1983, 1984, 1985, 2003), and primates (Visalberghi et al., 2003), few studies have focused on the responses of aquatic animals to novel foods. Hermit crabs make an excellent system to test hypotheses regarding

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the use of novel food items because they are generalist scavengers with incredibly broad feeding niches (Laidre, 2013) and live in areas characterized by spatial and temporal irregularity of food resources (Polis and Hurd, 1996). The marine intertidal zone inhabited by hermit crabs provides foragers with opportunities to encounter novel food items because currents and wave action carry offshore carrion into the intertidal zone (Britton and Morton, 1994; Polis and Hurd, 1996). These offshore carrion sources can include migratory or seasonably abundant species that are not a staple of the local environment, and thus can serve as novel food items for intertidal hermit crabs. Additionally, human influences, such as agriculture, urban development, and improper waste disposal (e.g., beach litter) can introduce novel foods into hermit crab foraging environments. Indeed, hermit crabs have been documented to consume novel foods including human wastes (Barnes, 1997) and even to consume conspecifics (Tran, 2014b). Additionally, they are known to be capable of rapid associative learning of the sensory cues provided by novel foods (Wight et al., 1990).

The nutritional benefits of novel foods, paired with the scarcity of adequate protein sources (e.g., carrion) in the intertidal zone (Polis and Hurd, 1996) make it worthwhile for hermit crabs to possess innate sensory mechanisms allowing them to discriminate between edible and inedible novel items upon first encounter. A previous study (Wight et al., 1990) has shown that hermit crabs will readily consume novel foods, and thus do not require associative learning to distinguish edible and inedible items encountered during foraging. The mechanisms by which they detect and assess the edibility of novel foods are likely innate sensory mechanisms that recognize general blends of common foraging cues within the odors emitted by novel foods (Schmidt and Mellon, 2010), such as amino acids or other naturally occurring metabolites (Carr et al., 1996). Indeed, classical studies of the chemical compositions of food items have shown that even distinct food items (such as beef and fish) can contain similar amino acid profiles and concentrations (Beach et al., 1943). It is, however, unknown what sensory organs (antennules, antennae, walking legs, etc.) or neural pathways are involved in the detection and recognition of novel food odors.

In regards to foraging behavior, little is known about the level of stimulus (odor) reinforcement that is needed to maintain behavioral reactions to these novel odors after the initial exposure. To my knowledge, no studies to date have addressed whether hermit crabs maintain their baseline levels of reaction to novel food odors over repeated, unreinforced exposures. In the context of novel food items and foraging, odor reinforcement would come from the animal detecting the novel food through some sensory input and then consuming the novel food. In contrast, sensory detection of the novel food item without subsequent feeding would constitute an unreinforced exposure. In the case of hermit crabs, reinforcement of food odor cues would likely entail the activation of olfactory receptors during initial stimulus detection (Tran, 2013) and then the subsequent activation of gustatory receptors during ingestion.

The objectives of this study were to (1) quantify the behavioral foraging reactions of intertidal hermit crabs to novel food odors, and (2) determine if reinforcement of the novel food odor is necessary for the animals to maintain their baseline reactions to the odor. I predicted that hermit crabs would (1) show foraging reactions to novel food odors upon first exposure, and (2) decrease the vigor of their foraging behaviors after repeated, unreinforced exposures.

## 2. Material and methods

### 2.1. Animal housing and maintenance

*Clibanarius digueti*, an abundant intertidal hermit crab from the Gulf of California, served as the study species. Animals were

acquired from a commercial distributor (A & M Aquatics, Lansing, MI), housed communally in 10 gallon glass housing tanks filled with artificial saltwater (ASW; Instant Ocean) under a 12:12 light:dark cycle, and fed 2–3 times weekly with pellet food (NewLife Spectrum). All ASW used in this report was maintained at a specific gravity of 1.022–1.024, pH 8.2–8.4 and a temperature of 23–27.5 °C. Animals were acclimated to these housing conditions for a minimum of two weeks prior to use in experiments. On the day before testing began, animals were transferred to experimental housing units consisting of 26 × 16 × 17 cm (L × W × H) plastic pet containers containing ASW and gravel substrate. Animals were housed in groups of 10 individuals during the experiments. Animals were not housed individually because (1) there were limitations in housing space in the lab and (2) the effects of isolation on the behaviors of these social animals were unknown. Although animals were housed in groups of 10, they were tested individually in all experiments.

### 2.2. Stimulus preparation

All stimuli, including ASW controls, were made fresh at the beginning of each experiment day and maintained on ice until use to preserve freshness. A known food odor (pellet) was extracted from the animals normal pellet food and used as a control in these experiments. This pellet odor represented a known odor because (1) the animals were repeatedly exposed to it during their housing in the lab, and (2) it has been shown to elicit strong and consistent foraging responses in this species (Tran, 2013). Pellet odor was made by macerating 1.0 g of food pellets in 100 mL ASW for 2 min and straining through medium filter paper. A novel food odor (beef) was made by repeating this same procedure, except substituting beef tissue for food pellets. Beef was purchased from a local vendor, cut into ~1.0 g pieces, frozen, and thawed until soft at room temperature on the day of use. Beef was used to make the novel odor because beef (1) is not a component of the normal diets of hermit crabs (i.e., the animals are not regularly exposed to it in nature), and (2) was not an ingredient of the pellet food used to feed animals during acclimation in the lab. As a result, animals should have possessed no learned associations linking beef odor with any prior feeding outcome, and thus all animals were presumed naïve to the odor of beef prior to use in these experiments. Because beef contains amino acids and muscle metabolites (Beach et al., 1943) which have been shown to be feeding effectors for crustaceans, I assumed that beef odors could be detected and assessed via the existing sensory structures of the hermit crabs.

### 2.3. Testing apparatus

The testing apparatus consisted of a 250 mL glass Erlenmeyer flask containing 250 mL ASW and clean gravel substrate.

### 2.4. Quantifying foraging behaviors

I used the procedures of Tran (2013) to quantify foraging behaviors. A single animal was placed into the testing apparatus and given a minimum of 15 min to acclimate. Following acclimation, 2 mL ASW were pipetted into the top of the apparatus using a glass pipette. The number of feeding movements (cheliped- and dactyl-to-mouth movements) that the animal exhibited was counted for three minutes. This count represented the pre-stimulus count. Following the pre-stimulus count, 2 mL of test odor were pipetted into the apparatus and the number of feeding movements was again counted for 3 min. This count represented the post-stimulus count. Movement Scores were calculated to be the number of post-stimulus feeding movements minus the number of pre-stimulus feeding movements (Johnson and Atema, 1986; Tran, 2013). Since hermit crabs often respond to overhead movements by retracting

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