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Risk-taking and risk-avoiding behaviors by hermit crabs across multiple environmental contexts

Daniel Gorman[a,b,*], Marilia N. Ragagnin[a], Ian D. McCarthy[c], Alexander Turra[a]

[a] Instituto Oceanográfico, Universidade de São Paulo, São Paulo, SP, Brazil
[b] Centro de Biologia Marinha da Universidade de São Paulo, Brazil
[c] School of Ocean Sciences, Bangor University, Bangor, United Kingdom

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ABSTRACT

Animal personality can affect individual fitness and the dynamics of populations. This study tested variation in risk-avoiding (emergence from shells) and risk-taking behaviors (abandoning shells) within a cohort of hermit crabs (*Clibanarius vittatus*) under a range of environmental stimuli. The startle response (SR) of individuals to predators (negative stimuli) and cues that signal new shells (positive stimuli) was measured under contrasting scenarios of shell condition (intact vs. damaged). The abandonment response (AR) of the same individuals was then measured following entrapment to further test consistency in individual behavior. SR varied according to stimuli and shell condition, with individuals showing a faster response to predators when inhabiting intact shells, than damaged shells that made them more vulnerable. Interestingly, the response to gastropod cues was faster when individuals were in damaged shells, possibly reflecting greater motivation to investigate new resources. When assessing the SR of individual subjects, strong correlations were observed across the different trial combinations (14 out of the 15), suggesting that the behavior of an individual under one set of treatment conditions, is a good predictor of its behavior under other conditions. AR similarly varied with shell condition, with crabs more likely to abandon damaged, rather than intact shells. Multivariate analysis linking these suites of behaviors (predator SR + gastropod SR + entrapment AR) highlighted consistent among individual variation in behavior driven by distinct responses to stimuli. Overall, we show that hermit crabs can exhibit unique personality traits that will influence their survival and fitness in environments where predation risk and resource availability vary over short spatial and temporal scales.

1. Introduction

Consistent among-individual variation in behavior (i.e., 'animal personality'), is a common feature of some invertebrate taxa including spiders (Kralj-Fiser and Schneider, 2012), aphids (Schuett et al., 2011), crickets (Rose et al., 2017), beetles (Schuett et al., 2018), bumblebees (Muller et al., 2010) and hermit crabs (Briffa et al., 2008). Behavior can vary as a result of differences in condition, energy reserves and size, and may lead to distinct and predictable responses by individuals that reflect different optimal behaviors within the same environment (Houston and McNamara, 1999; Mangel and Stamps, 2001). Understanding the spectrum of behavioral responses to common stimuli is essential to predict how organisms might adapt to environmental change (Schuett et al., 2018). The propensity for 'risk-taking' and 'risk-avoiding' behaviors within a population, for example, is likely to have implications for survival where selective pressures such as predation and resource availability vary over short spatial and temporal scales (de la Haye et al., 2012).

Hermit crabs are an excellent model for testing hypotheses about behavior, as they respond to a range of environmental cues that relate to predation risk (Gorman et al., 2015b; Rosen et al., 2009), shell acquisition (Billock and Dunbar, 2011; Tricarico and Gherardi, 2006), background colour and temperature (Briffa, 2013; Briffa and Twyman, 2011) and changes to their immediate physical environment (i.e., water level and salinity; Osorno et al., 2005; Shumway, 1978). In order to understand how individuals differ in their patterns of behavior (i.e., 'behavioral plasticity'; Mowles et al., 2012), it is necessary to obtain repeated measures from a cohort of individuals within a given scenario, and preferably across different contexts (review Sih et al., 2004). For hermit crabs, such behavioral variation can manifest as trade-offs, for example, a tendency to abandon shells might prove advantageous where disturbances such as burial and smothering are frequent, but might be detrimental where predation risk is high (Gorman et al., 2015b).

* Corresponding author at: Instituto Oceanográfico, Universidade de São Paulo, Praça do Oceanográfico, 191, 05508-120, São Paulo, SP, Brazil.
E-mail address: dgorman@usp.br (D. Gorman).

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The aim of this study was to test consistent variation in the behavior of hermit crabs *Clibanarius vittatus* (Bosc 1802) by examining how individuals differ in risk-avoiding and risk-taking behaviors. We assessed the behavior of individuals in terms of their startle response (SR) to both negative and positive stimuli (i.e., predators and gastropods, respectively); and their abandonment response (AR) to shells that become trapped (e.g., as can occur from disturbances such as storms); under contrasting scenarios of shell condition (intact vs. damaged shells). The idea to test SR under different shell condition scenarios was based on the hypothesis that the magnitude of this response would vary according to an individual's vulnerability to predation and motivation to acquire an intact replacement (i.e., both presumably higher in a damaged shell). We similarly hypothesized that the risk-taking AR of individuals might relate to the trade-off between increased immediate exposure of abandoning a shell and the longer-term advantages of finding a replacement. Overall, our goal was to identify predictable variation in the behavior of *Clibanarius vittatus* as has been demonstrated for other intertidal hermit crabs (e.g., *Pagurus bernhardus*; Briffa et al., 2008) and which is being increasingly recognised as animal personality within certain invertebrate taxa.

2. Material and methods

2.1. Study animals and behavioral context

The study involved the common hermit crab *Clibanarius vittatus,* which occurs throughout the intertidal and shallow waters of the western Atlantic (Forest and Saint Laurent, 1967). Along the southeastern coast of Brazil, this species has an intrinsic association with the empty shells of the gastropod *Stramonita haemastoma* (Linnaeus, 1767), which it uses as a domicile shell (Turra and Denadai, 2004; Turra and Leite, 2002). The species often aggregates at the mangrove-mud interface (Turra et al., 2000) where predation by large swimming crabs such as *Callinectes danae* (Smith, 1869) can be high (Gorman et al., 2015b) and physical disturbance such as burial and entrapment is common (Gorman et al., in press). Given variation in the immediate (e.g., predation) and longer-term risks (e.g., starvation) that individuals face, they can exhibit differences in 'risk avoiding' (retracting into shells) and 'risk taking' behaviors (abandoning shells; Gorman et al., 2015a) which are modulated by environmental factors. Using these complementary responses, our goal was to demonstrate consistent among-individual variation in behavior across multiple environmental contexts that might reflect their ability to cope with changes in predation risk and resource availability.

Experiments involved sixty hermit crabs of a similar size (mean ± SD 7.4 ± 2.2 mm shield length) that were collected from an intertidal area of Araçá Bay, Brazil (23°49′S 45°24′W). Given the uniform size of the cohort and lack of published reports of age-specific variation in behavior, this factor was not considered. Initial field measurements of startle response (SR) were recorded for comparison with experimental results (see following sections). Collected subjects were divided randomly into three experimental blocks ($n = 20$ individuals) and transported to a seawater aquarium system at the Marine Biology Center of the University of São Paulo. The identity of each individual was maintained throughout the study by housing them in small round plastic cups (12 cm height × 10 cm ø) perforated with holes to enable seawater exchange.

2.2. Experimental trials, stimuli and shell condition

Experimental trials were designed to test individual variation in risk-avoiding and risk-taking behavior against a background of shell condition (intact vs. damaged shells). Risk-avoiding behavior was assessed using the Startle Response (SR) of individuals exposed to predator and gastropod cues that are common features of the crabs' natural environment (Fig. 1). SR is widely used in studies of hermit crab behavior (Elwood et al., 1998; Mowles et al., 2012), and is typically measured as the time taken for an individual to emerge from its shell after disturbance (see Briffa et al., 2008). In the present study, subjects were upturned (aperture facing up) using forceps and touched with a rod so that they completely withdrew into their shells. The SR duration was recorded in seconds, as the time taken for each individual to emerge from the aperture and turn its shell over to the normal position (right-side up, aperture facing down) using a digital stopwatch and multiple concurrent observers.

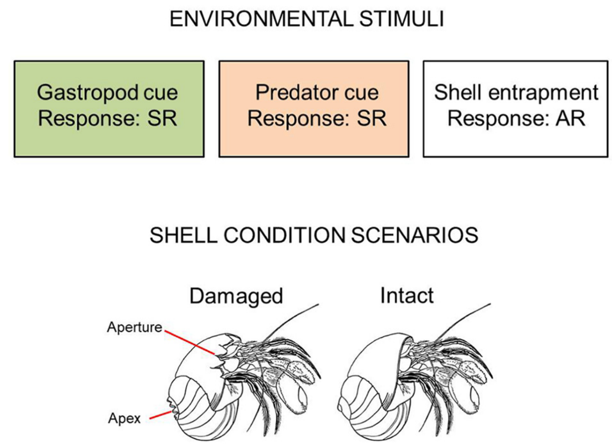

Fig. 1. Schematic showing the environmental stimuli and the shell condition scenarios tested through repeated trials (Image of hermit crab, modified after Florida Center for Instructional Technology, 2018).

The choice of stimuli was based on the overwhelmingly negative response of hermit crabs to predators (Kuhlmann, 1992; Rittschof and Hazlett, 1997; Scarratt and Godin, 1992) and their positive response to cues that signal gastropod predation events, where new shell resources are often acquired (Laidre and Greggor, 2015; McLean, 1974; Rittschof, 1980; Souza et al., 2016). The predator treatment was prepared by placing 8 live *C. danae* into 20 L experimental tubs for 30 min (i.e., method adapted from Hazlett, 1997). Gastropod cues were prepared by immersing the flesh of 10 crushed *S. haemastoma* (animal and shell) diluted in identical 20 L experimental tubs.

The influence of shell quality was evaluated through repeated trials using the same individuals housed in intact vs. artificially damaged shells (Fig. 1). Damaged shells had the apex crushed using a small bench vice and the aperture broken using pliers to reflect the typical degree of shell damage observed across the study area (Turra, 2003; Turra et al., 2005). Intact shells were of sufficient size to permit crabs to completely retract inside, while damaged shells greatly increased the vulnerability of individuals to predation (i.e., especially when the shell apex was facing up). After every trial involving a damaged shell, subjects were provided an intact replacement shell of a similar size and given a rest period of 24 h before undergoing the next trial.

Exposure to stimuli in the SR trials was done by placing individuals and their plastic cups into the large 20 L experimental tubs in which the various treatments had been prepared. Each experimental block (20 individuals) was randomly split into two groups; half in intact shells and the other half in damaged shells prior to being exposed to stimuli. For each trial, half of the subjects within the given block were placed into identical tubs with no stimuli as a control. After trials, cups were rinsed thoroughly with fresh seawater and individuals returned to aquaria to be given a rest period of 24 h between successive experiments. Crabs were fed commercial grade fish food (a single pellet per individual) every 24 h following trials to prevent changes in behavior due to hunger. Any food not consumed by the next morning was removed. Because trials involved exposure to stimuli and shell condition treatments in a randomized order, we did not consider temporal autocorrelation. Overall, a single SR value was obtained for each individual