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Subjective resource value and shell abandoning behavior in hermit crabs

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ABSTRACT

Understanding the factors that motivate animals to hold or abandon a valuable resource is a central goal of behavioral ecology, the study of which will grow more important in the face of increasingly frequent extreme events. We compared the shell-abandoning behavior of the sympatric hermit crabs *Clibanarius antillensis* and *Pagurus criniticornis* in response to simulated burial and entrapment by rocks and other debris. While these hazards are relatively common in dynamic intertidal habitats, the frequency and severity of such disturbance are increasing due to human activity. While both species exhibited shell-abandoning behavior in response to experimental burial, it was far more prevalent for the soft-bottom dwelling species *P. criniticornis* (90%) when compared to the rocky bottom inhabitant *C. antillensis* (55%). Simulated entrapment experiments highlighted further differences in species response, with the decision to abandon domicile shells again far more common for *P. criniticornis* (80%) than it was for *C. antillensis* (10%). Given the tendency for *P. criniticornis* to abandon its shell, we subsequently focused on this species to test specific hypothesis about subjective resource value in hermit crabs. There was no difference in the tendency for this species to abandon optimal or sub-optimal (poorly-fitting) shells when faced with the immediate and potentially fatal risk of burial. This contrasted the response seen under conditions of entrapment, whereby individuals inhabiting sub-optimal shells abandoned them more rapidly and in greater numbers than those inhabiting optimal shells. Combining these two outcomes, we suggest that hermit crabs subjectively assess shell-value and respond according to the nature of the disturbance and its associated risks (i.e., high-value shells are abandoned in minutes under conditions of burial; but are held for hours under the less severe conditions of entrapment). In effect, the results show that extrinsic environmental cues can be just as important to decision making processes as those intrinsic cues that govern an animal's physiological condition. The contrasting behavior of the two hermit crabs to the movement of mud and other debris may lead to a higher survivorship of *P. criniticornis* than *C. antillensis* where activities such as dredging and harbor construction are intensifying along developing coastlines.

1. Introduction

Given forecast changes to earth systems over the coming decades (Hooper et al., 2005) an aspiring field of research will focus on the behavioral adaptations of animals to dwindling resources and greater environmental instability (Dill, 1987). Defining the point at which individuals choose conflicting outcomes to balance their intrinsic physiological needs (e.g., nutrition, mates, competition, and risk of combative injuries) with their continued survival in the face of environmental change (e.g., escalating levels of disturbance, altered ecological niches, and contracting distributions) will be vital for our ongoing understanding of community and ecological resilience. The choices animals make about whether to hold onto, or abandon a resource, depends on its 'subjective value' (sensu, Briffa and Elwood, 2001; Briffa and Elwood, 2002). This judgment is typically governed by a complex process whereby individuals evaluate external cues that have direct implications for fitness or survival (Parker and Stuart, 1976). Up until now, the majority of studies into this type of subjective behavior have tended to focus on the 'internal' physiological state (e.g., acquisition of food and mates; (Dennenmoser and Thiel, 2007; Kelly, 2008; Mohamad et al., 2010) and maintaining adequate shelter; (Arnott and Elwood, 2007; Doake and Elwood, 2011; Lindstrom and Pampoulie, 2005). Enquist and Leimar (1987) demonstrated that for many taxa, hungry individuals place a higher value on a food resource then satiated animals, fighting longer and harder. Satiated animals benefit from abandoning the resource so as to avoid the possible risk of injury or death (Arnott and Elwood, 2008). There has been comparatively less work done to investigate the decisions animals make in relation to 'external' environmental factors. The choice, of whether to hold or abandon a valuable resource under conditions of more frequent and severe environmental perturbation, may have consequences that either increase or undermine an animal's chances of survival.

Hermit crabs offer an excellent opportunity to test hypotheses related to subjective resource value as they are easy to manipulate with respect to their key resource; the gastropod shell (see, Hazlett, 1981; Turra and Denadai, 2004). The high value individuals place on an 'optimal' shell can influence a wide range of behavioral traits related

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to mating, fighting, feeding, and even escaping from predators (Hazlett, 1997; Hazlett and Rittschof, 2000; Hazlett and Rittschof, 2005; Huntingford, 1992; Rittschof et al., 1992). Although hermit crabs must upgrade their shell periodically for growth (Childres, 1972), the 'naked' inter-period is characteristically brief (Billock and Dunbar, 2009; Laidre, 2012) because without it, crabs have no protection for their soft abdominal exoskeleton and risk desiccation (for intertidal and terrestrial species), physical injury, and predation (Arnott and Elwood, 2007). Hermit crabs inhabit dynamic coastal environments that are regularly affected by storms, king tides and floods and have thus evolved a suite of behavioral responses to deal with these harsh conditions, e.g., the ability to extricate themselves, and their shell from the sediment if buried (Barnes, 2002; Rebach, 1974; Taylor, 1981; Turra and Denadai, 2003) or the capacity to adopt a sessile lifestyle if trapped (Gherardi, 1996; Hazlett, 1981; Manjon-Cabeza and Raso, 1995; Rodrigues et al., 2000; 2002). The circumstances under which individuals will fully abandon shells, however, tend to be restricted to those that pose a real and immediate risk of injury or death (Gorman et al., in review; Hinchey et al., 2006). Within estuarine and some coastal environments, such extreme conditions can occur when sediment becomes re-suspended by waves and deposited rapidly to form layers from a few centimeters to up to a few meters deep (Calliari and Fachin, 1993; Nichols, 1984; Wells, 1983; Yang et al., 2005). Similarly, the movement of rocks and other large debris (e.g., logs and branches, etc.) during storms or more infrequently floods can trap slow-moving organisms including hermit crabs. Faced with such hazards, and especially where human activities have increased the frequency and scale of such disturbance, species that lack adequate behavioral adaptations face a real and present risk of death (Easterling et al., 2000) through asphyxiation (burial) or starvation (entrapment).

Comparing the response of hermit crabs to differing levels of environmental risk (e.g., burial vs. entrapment) provides an excellent test of the extrinsic factors that moderate decision making and may help to explain whether habitats shape the response of individuals. Hermit crabs make predictable decisions based on the quality of their shells (e.g., abandoning low-quality ones for higher quality specimens; Arnott and Elwood, 2007; Briffa and Elwood, 2001; Elwood, 1995; Hazlett, 1981), and undergo strategy shifts in response to intrinsic stimuli, e.g., during shell fights when subordinate crabs are 'forced' or 'convinced' to abandon their shells by dominant individuals (Hazlett, 1981). Few studies have investigated behavioral variability in the response of crabs to their physical environment (but see for exceptions; Cote et al., 1998; Hahn, 1998); with even fewer examining the interacting effects of physical disturbance and learned behavior. Gorman et al. (in review) recently highlighted the importance of physical shell attributes, chemical cues and learned behavior as drivers of shell abandoning in *Pagurus criniticornis*. It is highly likely that extrinsic environmental cues play just as important a role in the decision making processes as those intrinsic cues that govern an animal's physiological condition. Because subjective value relates directly to an individual's fitness (Parker and Stuart, 1976), the immediate and potentially life-threatening situation of being buried alive (Chandrasekara and Frid, 1998; Cruz-Motta and Collins, 2004) would presumably overwhelm even the highest subjective value (e.g., an optimal shell) to elicit a profoundly differing response (both in terms of rate and tendency of abandonment) when compared to the less immediate risks posed by entrapment that may warrant persisting with such a high-value resource. Using the response of hermit crabs as a general model to examine the decisions that animals make in response to a changing environmental may facilitate a broader understanding of similar processes in multiple marine and terrestrial taxa.

The aim of this study was to test hypotheses about risk-based decisions (i.e., rated to microhabitats) and subjective resource value (i.e., shell adequacy) in two species of hermit crab, and to use this information to assess their relative susceptibility to environmental disturbance. Beyond the examples given above, a broad literature search returned very few studies on shell abandoning behavior of these animals (but see, Appel and Elwood, 2009; Elwood and Appel, 2009); a concerning discovery given the increasingly frequent and extensive scale of coastal disturbance (e.g., dredging, land reclamation and increased coastal erosion; Airoldi and Beck, 2007) that increase the risks of burial and entrapment for crabs and other species. Given that the threat of burial and entrapment will differ across a spectrum of estuarine and coastal habitats, we theorized that benthic fauna inhabiting different intertidal zones may exhibit contrasting responses with respect to resource holding potential and subjective resource value (sensu, Gherardi, 2006). To this end, we utilized two sympatric hermits; *Clibanarius antillensis* and *P. criniticornis* to test the null hypotheses that there would be no difference in the proportion of individuals emerging from the substrate following simulated burial. Entrapment by rocks and other debris displaced during storms or similar disturbance, presents further risks to hermit crabs but ones that are unlikely to present an immediate risk of death. We thus proposed that hermit crabs would respond more slowly (in relation to burial), and that the time taken for individuals to abandon trapped shells may depend on the subjective value they place on these resources. We tested a second hypothesis that there would be no difference in the behavior (a qualitative response) and the proportion of individuals of both *C. antillensis* and *P. criniticornis* that abandon their shells in response to simulated entrapment (noting that neither of these species have never been reported to occupying sessile shelters). Given that the prevalence of shell abandoning is likely to directly relate to the subjective value individuals place on their domicile shells, we examined the effect of shell adequacy (i.e., well-fitting 'optimal' shells vs. poorly-fitting 'sub-optimal' shells) on the response of *P. criniticornis* under the same conditions of simulated burial and entrapment. We tested if individuals inhabiting optimal shells would attempt to hold these resources for a longer period of time and in greater proportions than those in sub-optimal shells.

2. Material and methods

2.1. Subjects, collection and housing

This study focused on *C. antillensis* (Stimpson, 1859) and *P. criniticornis* (Dana, 1852) two common species of hermit crab that are widely distributed throughout intertidal and shallow subtidal waters of the western Atlantic (Forest and Saint Laurent, 1967). In the region surrounding Araçá Bay (São Sebastião, state of São Paulo, south-eastern Brazil), the species coexist and exhibit partial resource competition for the shells of the gastropod *Cerithium atratum* (Turra and Denadai, 2004; Turra and Leite, 2002). The two species demonstrate some degree of microhabitat partitioning, with *C. antillensis* occupying upper intertidal areas comprising coarse sand and rocky substrates more frequently than *P. criniticornis* which predominates in the muddy substrates characteristic of lower intertidal areas (Turra et al., 2000). As a consequence, burrowing behavior has been shown for *P. criniticornis* but not for *C. antillensis* (Turra and Denadai, 2003). Although these species are presumed to be similarly affected by environmental perturbations such as burial and entrapment, they are likely to present differing responses with respect to shell abandoning behavior that relate specifically to their microhabitat occurrence. Approximately 200 individuals of each species and of a similar size (3–4 mm shield length) were collected from Araçá Bay (23°49′S 45°24′W) two days prior to experimentation, and were maintained in plastic containers supplied with circulated seawater.

2.2. Species response to simulated burial and entrapment

Two separate experiments were designed to simulate the effect of burial and entrapment on the shell abandoning behavior of *C. antillensis* and *P. criniticornis*. The burial experiment incorporated five replicate blocks comprising 10 individuals of each species, with manipulations