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2014

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.

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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

done in small round plastic cups (12 cm height × 10 cm ø). Sediment collected at sites adjacent to crab collection areas in Araçá Bay (top ~5 cm surface layer) was liquefied in seawater within a second plastic container to produce a 10 cm deep layer of fluid mud that was poured rapidly onto the crabs in the experimental cups to simulate sudden burial. Observations of mud inundation within the study area show that layers of about 10 cm are periodically deposited, especially in summer months (Alexander Turra, Pers. Obs.). Sedimentation occurred within 1 min after which the number of crabs emerging from the sediment with and without shells was recorded for a duration of 5 min. Crabs that remained buried after this time faced a high probability of death through asphyxiation (due to sediment compaction), thus all individuals were dug up to prevent mortality, with the number that retained and abandoned their shells recorded to provide overall proportions for each possible outcome (i.e., emerging +S, emerging −S, remaining buried +S and remaining buried −S). Data were analyzed using analysis of variance (ANOVA) in which the five replicate 'blocks' (treated as orthogonal and random) were nested within the treatment 'species' (fixed and orthogonal).

The response of C. antillensis and P. criniticornis to entrapment was simulated by the immobilization of their domicile shells using 'Super Bonder' cyanoacrylate instantaneous glue (Ellsworth Adhesives, Germantown, U.S.A.) in combination with inversion (i.e., placing them upside-down to facilitate maximum exposure of shell aperture). Shell attachment was achieved prior to the commencement of the experiments by gluing circular glass disks (4 cm diameter) to the top of shells that housed individual crabs. Upon commencement of the experiments, the 20 replicate shells for each species were turned upside-down so that they were supported by the glass disks before being allocated to random interspersed glass aquaria (50 × 30 × 40 cm) that were supplied with circulated seawater. The behavioral response was then followed for a period of 16 h, with qualitative descriptions recorded as well as number of crabs returning each of the two possible outcomes (i.e., holding or abandoning their shells).

2.3. Resource value judgments by P. criniticornis

A second suite of experiments was done to evaluate the effect of relative shell size (shell adequacy sensu Vance, 1972) as a predictor of shell abandoning behavior by P. criniticornis under conditions of simulated burial and entrapment. To produce the two desired treatments; (1) crabs having 'optimal' shells, and (2) crabs having 'sub-optimal' shells; individuals were removed from pre-existing shells by gently cracking them, with only non-injured crabs used for the experiments. These naked individuals were allocated at random to two subgroups, the first 60 offered a large assortment of empty C. atratum shells (n > 200) of varying sizes; while the second 60 individuals were offered relatively small shells (shell length 1/3 of optimal shells). Gastropod shells were prepared by boiling live individuals and removing the flesh, rinsing the shells several times in alcohol and seawater and air-drying prior to them being offered to crabs over a 48 h period within undisturbed aquaria supplied with circulated seawater. The available shells in the sub-optimal treatment were relatively small in relation to crab size, so that individuals were not able to completely retract their entire body inside and thus remained with chelae exposed at the shell aperture (see shell adequacy index, Turra, 2003). As a further validation of our treatment criterion (optimal vs. sub-optimal) we assessed a subset of individuals using the optimal shell length equation of Gherardi (2006). The first experiment subjected 10 crabs × six replicate blocks × the two treatments (i.e., $n = 60$ optimal shells and $n = 60$ crabs in sub-optimal shells) to simulated burial and was analyzed as per the methods described in Section 2.2.

The effect of shell adequacy on the shell abandoning behavior of P. criniticornis was also investigated in response to entrapment. Shell adequacy treatments (optimal vs. sub-optimal shells) were prepared as above and entrapment was simulated as per the methods described in Section 2.2. The 20 individual animals employed to each treatment were randomly positioned in the experimental aquaria and the shell abandoning responses were followed at 2 h intervals over a period of 16 h.

3. Results

3.1. Species response to simulated burial and entrapment

For both species of hermit crab, the greater proportion of individuals emerged from the substrate within 5 min of being buried (Fig. 1). Those that did not were extricated from the sediment in time to prevent death through asphyxiation. The results demonstrated clear differences in the behavioral response of the two species (ANOVA 'Species × Treatment' term; $F_{3, 28} = 10.57$; $P < 0.001$) with the proportions of P. criniticornis emerging from the sediment with and without their shells indistinguishable, but significantly greater than those remaining buried (SNK tests: emerged +S = −S > buried +S = −S). This differed substantially from the outcomes for C. antillensis whereby the greatest proportion of crabs remained buried inside their shells (46%) and those that emerged with their shells were significantly more numerous than those without (SNK tests: buried +S = emerged +S > emerged −S > buried −S). It is noteworthy that no individual C. antillensis remained buried without a shell.

The simulated entrapment experiment highlighted qualitative similarities in the response of both crab species (i.e., their procedural investigation of environmental cues; described following) but the final outcome after 12 h of observation revealed clear differences in the tendency of the two species to abandon their shell (10% of C. antillensis vs. 80% of P. criniticornis). Upon commencement of the experiment all individuals of both species were completely retracted into their shells, but after a few minutes they initiated movements at the shell aperture (extending chelae), before exiting to crawl on the shell and assess what was limiting their movement. Crabs then attempted to dislodge their shells using their chelae and ambulatory legs as leverage against the plastic disks, before partially or totally (less frequently, 10%) leaving the shell aperture completely to search for holding surfaces (anchoring points). During this process, the uropod of most individuals remained in contact with the columella of the shell, and the fourth and fifth pairs of
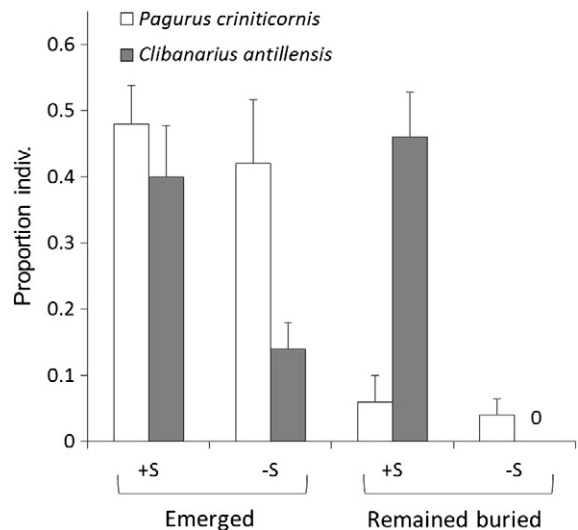

Fig. 1. Proportion of hermit crabs (Pagurus criniticornis and Clibanarius antillensis) that yielded each possible experimental outcome as a response to simulated burial; +S = observed with shell, −S without shell. Data reflects mean ± SE of the mean from $n = 5$ replicated experiments.
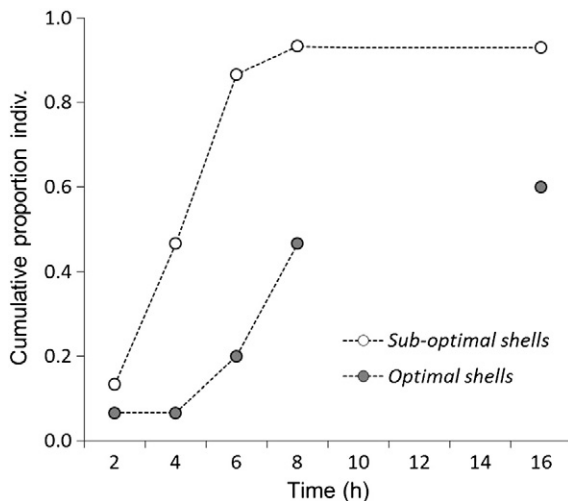
pereopods were used to hold and support the individual at the shell aperture. The movements typically traced the orientation of the shell spiral toward the shell apex and counter-spiral side before ending on the shell body whorl. At the conclusion of these processes, two outcomes were possible, either; (1) crabs remained immobile at the shell aperture with their chelae and walking legs exposed but moving their mouthparts, antennas and antennules, alternating periodically with the shell-assessment behavior described above; or (2) crabs abandoned their shells.

3.2. Resource value judgments by P. criniticornis

There was no evidence that shell adequacy (optimal vs. sub-optimal shell size) influenced the proportion of *P. criniticornis* emerging from the sediment under conditions of simulated burial. Analysis revealed no interaction between 'Adequacy × Treatment outcome' ($P = 0.520$), no main effect of Adequacy ($P = 1.000$), but a significant effect of treatment outcome (ANOVA; $F_{3, 35} = 52.04$; $P < 0.001$; S-N-K comparisons; emerging $+S$ > emerging $-S$ > remaining buried $+S = -S$). There were marked differences in the shell abandoning behavior of individual *P. criniticornis* inhabiting shells of different adequacy under conditions of simulated entrapment (Fig. 2). Comparing the cumulative proportion of crabs that abandoned their shells over time revealed those in sub-optimal shells did so more rapidly and in overall greater numbers than did individuals in optimal shells (maximum difference observed after 6 h of observation). After a period of 16 h, 93% of individuals had abandoned sub-optimal shells while only 60% had abandoned optimal shells.

4. Discussion

The decision of hermit crabs to abandon their shells varied between species and was strongly dependent on the type of hazard the animals faced. Under conditions of burial by fluid mud similar to that which poses a hazard in many intertidal environments (Calliari and Fachin, 1993), the greater proportion of individuals of both species were able to rapidly emerge from the sediment (55% of *C. antillensis* and 90% of *P. criniticornis*). The puzzling result however, was the relatively large proportion of *C. antillensis* that remained in their buried shells and would have subsequently died through asphyxiation (46%). There were also marked differences in the ability of the two species to emerge still possessing their domicile shell which would likely influence

relative rates of post-emergence survival. Nonetheless, it is clear that shell-abandoning behavior represents a generalized strategy employed by these intertidal species in response to sudden and unexpected burial. While the proportion of *P. criniticornis* emerging with and without their domicile shells was not significantly different (and averaged ~45%), the proportion of *C. antillensis* emerging without shells was significantly lower than those emerging still holding their shells. It was also interesting that no *C. antillensis* remained buried without a shell, while 4% of *P. criniticornis* did so and would have presumably died as a result. Together, these outcomes suggest that individual *C. antillensis* that find themselves unable to extract their shells from the sediment (i.e., an issue of drag potential; Osorno et al., 2005) may attempt to hold these resources despite the imminent risks. We can only speculate as to the cause of such species-specific behavioral responses, however they are likely to reflect the contrasting estuarine and coastal microhabitats in which the two species predominate; the soft-bottom species *P. criniticornis* being comparatively better adapted to deal with sudden burial (e.g., along with profound ability to successfully extract its domicile shell; Barnes, 2002; Turra and Denadai, 2003). The prevalence of shell abandoning behavior for this species has also been shown to relate to previous experience (Gorman et al., in review) and it is possible that the subjects had undergone recent burial in the field (Daniel Gorman, Pers. Obs.). In contrast, *C. antillensis* does not display burrowing behavior (Turra and Denadai, 2003) and its preference for harder substrates would make it less likely to encounter situations where it must rapidly extract itself from fluid mud. Variation in the burial response of the two crab species is likely to have consequences for rates of survivorship if burial becomes a more prevalent disturbance in their environments (e.g., through human activities that increase the scale and rate of sediment deposition).

The behavioral response of hermit crabs to simulated entrapment (e.g., replicating the movement of rocks and other debris by storms and tides; Hughes and Chiu, 1981) demonstrates further differences between the two species examined. Over a period of 16 h, there was a profoundly greater tendency for individual *P. criniticornis* to abandon their shells (80%) when compared to *C. antillensis* (10%). While a sessile lifestyle may be a successful strategy for some species of hermit crab (Gherardi, 1996; Hazlett, 1981; Manjon-Cabeza and Raso, 1995; Rodrigues et al., 2000; 2002), this has never been recorded for *C. antillensis* (i.e., it lacks the morphological adaptations for filter-feeding). Instead, our findings more likely reflect the greater tendency for this species to retain what it deems a high-value resource, in a similar way to that described for other marine and terrestrial taxa (e.g., ranging from crabs to crayfish and rats to chimpanzees; Enquist and Leimar, 1987). The comparatively low-quality of empty shells on offer within upper intertidal environments (Scully, 1979) in which this species predominates, could motivate individuals to hold this valuable resource despite the risks. The response of *P. criniticornis* to entrapment on the other hand, is to rapidly abandon its shell, a decision that may be partially understood by the higher activity (Turra and Denadai, 2003) and greater exploitative ability of this species when seeking a replacement shell (Turra and Denadai, 2004). It may also involve a complex decision making process that balances the immediate risks of exposure with the expected energetic requirements of finding another empty shell given their scarcity (Fotheringham, 1976b; Kellogg, 1976). To address the strong species-specific response to entrapment, we propose further experiments in which upper and lower intertidal species (i.e., inhabiting muddy vs. rocky substrates) are translocated to test the effect that habitat may have on crab behavior over the short, medium and long term.

Despite the differing outcomes for the two species, our results demonstrate similarities in the initial behavior of these two hermits that may be generic to estuarine or coastal dwelling crabs. Hermit crabs have been shown to assess their physical environment through visual and tactile investigation (Jackson and Elwood, 1989; Reese, 1969) and to respond accordingly by initiating adaptive motivational

Fig. 2. Effect of shell adequacy (sub-optimal vs. optimal shells) on the dynamics of shell abandoning in the hermit crab *Pagurus criniticornis* under conditions of simulated entrapment. Note; that no data was available for the time intervals; 10, 12, and 14 h and thus there is no line defining the change in cumulative proportion for individuals in optimal shells for this period.

changes that lead to strategy shifts (Tricarico and Gherardi, 2007). The qualitative descriptions we provide in this study show that these two species undertake a remarkably similar process of assessing how they are trapped, before deciding on a particular course of action. We encourage future studies that examine in more detail the behavioral responses of hermit crabs to entrapment (e.g., movements and motivational strategies such as attempts to dislodge shells) that may provide valuable insights into decision-making processes in other taxa.

Assessments of resource value involve a complex process in which environmental cues are correlated with some expected gain in fitness for the animal (Parker and Stuart, 1976). Our data provide insights into the tradeoffs that individual hermit crabs make between the environmental risks of holding a high-value shell (i.e., possible death from asphyxiation) and the longer-term hardships faced as a consequence of abandonment (i.e., predation, desiccation, physical damage, and even cannibalism). As hermit crabs subjectively evaluate a shell with respect to the level of room it provides and thus the protection it affords (Arnott and Elwood, 2007; Briffa and Elwood, 2001; Elwood, 1995; Hazlett, 1981) an optimal shell would constitute a higher-value resource than a sub-optimal one that limits growth (Angel, 2000; Bertness, 1981; Fotheringham, 1976c; Markham, 1968; Turra, 2003), fecundity (Childres, 1972; Fotheringham, 1976a), exacerbates predation risk (Angel, 2000) and physiological stress (Reese, 1969; Taylor, 1981). It follows then that crabs possessing optimal shells would be more likely to hold onto these and maintain them under all but the most severe environmental conditions. Indeed, we showed that the response of *P. criniticornis* to the immediate risk of burial was almost universal abandonment of their shells irrespective of adequacy. Burial appears to trigger a response that over-rides any form of subjective value for nearly all individuals. This contrasts the less severe and immediate condition of being trapped, whereby individuals inhabiting optimal shells displayed a profoundly slower and less complete tendency for abandonment than those in sub-optimal shells (60% cf. 93% respectively after 16 h). Similar motivational trade-offs have been observed for crabs exposed to electric shocks whereby individuals demonstrate a lower tendency to abandon preferred shell species (Elwood and Appel, 2009). In effect, extrinsic environmental cues appear to be just as important to decision making processes as intrinsic cues that govern an animal's physiological condition. As earths systems alter because of global and anthropogenic change, it will become increasingly important to understand the behavioral responses of animals to changing environmental conditions both on a local (e.g., pollution, eutrophication and sedimentation in the marine environment) as well as a global scale (e.g., climate change, global warming and acidification).

As a side to this study, the abandonment response of hermit crabs to simulated burial and entrapment may have practical application for future studies that require prior removal of crabs from their shells. Up until now studies have tended to rely on several undesirable methods for removing crabs from their shells, ranging from; immersion in tepid water or breaking shells open using blunt instruments (Turra and Leite, 2003), to applying direct heat using a flame (Hahn, 1998) or soldering iron (Cote et al., 1998). There has been no proposed method that combines the two desirable characteristics; (1) rapid removal without causing physical and physiological injury, and (2) preservation of shells for their subsequent reuse. Our observations of the high emergence of individuals (especially *P. criniticornis*) after just a few minutes of burial, suggest that methods based on this approach could be very useful in studies requiring large numbers of naked crabs. These procedures would be very interesting if it is the intention to return crabs alive to the sea after experimentation or evaluation of population parameters. Therefore, burial, arresting, or a combination of both may be employed as an efficient method to remove hermit crabs from shells in a way that conforms to current and future animal ethics standards.

In conclusion, we demonstrate that the decisions of hermit crabs to abandon their key resource differ among species and may relate to the type of environmental disturbance faced along with its associated risks. The drivers of such species-specific variation appear to relate to the differences in the way soft- and hard-bottom species deal with burial and entrapment and the subjective value that they place on their domicile shells (probably an issue of scarcity; Fotheringham, 1976b). The ability of *P. criniticornis* to rapidly emerge after burial and the elasticity in the value it places on shells of varying quality, may give it an advantage in areas where increasingly frequent storms, land reclamation, harbor developments and high rates of erosion are leading to accelerated rates of sediment accumulation (Thrush et al., 2003). In contrast, the high value that *C. antillensis* appears to place on its domicile shell may increase its susceptibility to natural and anthropogenic disturbance. In preparation for the dramatic changes expected in coastal zones over the coming decades (Airoldi and Beck, 2007; Lotze et al., 2006) we suggest that studies into the value marine and estuarine animals place on resources and ecosystem services will become a broadening research priority. Understanding the conditions under which animals balance the intrinsic needs of holding a high-value resource against the extrinsic risks posed by the external environment will become an increasingly important goal given limiting resources and the elevated levels of disturbance along developed and developing coastlines.

Acknowledgments

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