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PRIMARY RESEARCH PAPER

What motivates hermit crabs to abandon trapped shells? Assessing the influence of shell value, olfactory attractants, and previous experience

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Abstract Hermit crabs finding themselves in a trapped shell face a critical decision that will require an assessment of the benefits of abandonment against the increased risks of predation and desiccation. This study investigates factors that influence the rate of shell abandoning by common intertidal hermit crabs. We firstly established that the mud inhabitant, *Pagurus criniticornis*, exhibits a greater tendency to abandon shells when compared to its neighbors *Pagurus brevidactylus* and *Clibanarius antillensis*. We subsequently conducted a series of experiments on this species to assess the relative influence of (1) gastropod shell type, (2) shell adequacy, (3) shell condition, (4) olfactory attractants, (5) previous experience, and (6) shell acclimatization. *P. criniticornis* abandoned very small shells faster than optimal (well-fitting) specimens and damaged shells faster and more completely than intact specimens. Crabs exposed to olfactory cues (*Cerithium atratum*) were 15% more likely to abandon their shells than unexposed individuals. Similarly, individuals that had undergone previous abandonment experience and those given longer acclimatization periods (30 vs. 2 days) showed rates of abandonment that were 18 and 28% greater than contrasting treatments. The results can be used to aid our understanding of motivational behavior in invertebrates and other animals that inhabit temporary or ephemeral shelters.

Keywords White spotwrist · *Pagurus criniticornis* · *Clibanarius antillensis* · *Pagurus brevidactylus* · Subjective resource value · Shell occupancy

Introduction

Hermit crabs exhibit predictable behaviors related to the selection, acquisition, and maintenance of domicile shells (i.e. most notably relating to combative interactions; Huntingford, 1992; Rittschof et al., 1992; Hazlett, 1997; Hazlett & Rittschof, 2000; 2005; Arnott & Elwood, 2007; Tricarico & Gherardi, 2007). They also integrate a range of information sources to make complex choices in relation to external environmental stimuli that influence fitness and survival, e.g., memory of potentially painful events (Appel & Elwood, 2009a), conspicuousness of shell color with respect to background (Briffa & Twyman, 2011), and shell cripticity vs. predation risk (Briffa et al., 2008a). Less work has been done to examine behavior that balances

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the costs and benefits of relinquishing shells under contrasting situations (e.g., increased risk of predation vs. avoiding nutritional or reproductive constraints).

Hermit crabs typically abandon shells only when encountering a better quality replacement (Elwood & Stewart, 1985; Jackson & Elwood, 1989), losing a competitive interaction (Dowds & Elwood, 1983), experiencing irritation or noxious stimulus (Elwood & Appel, 2009), or when a domicile shell becomes buried or trapped (Turra & Gorman, 2014). Cross-situational testing has shown that hermit crabs often demonstrate individual and differing responses (i.e., behavioral consistency as well as plasticity; Briffa et al., 2008b), a phenomenon that helps to explain the evolution and maintenance of behavioral variation (see Sih et al., 2004). Thus, there is likely to be considerable inter- and intra- species variation in the willingness of crabs to abandon shells depending on contrasting levels of perceived advantage or risk (Briffa, 2013). Such variation can generate tradeoffs; for example, a greater tendency to abandon trapped shells might prove advantageous where environmental perturbations are frequent, but might be inappropriate where predation is high (Gorman et al., In review). Consistent individual variation in animal behavior, seen across a range of correlated categories or ‘contexts’, can indicate the presence of behavioral syndromes which are repeatable characteristics that in hermit crabs have been used to represent personality (see Mowles et al., 2012).

Physical disturbances in bays and other coastal environments (e.g., storms, floods, and high amplitude spring tides) often displace small boulders, rocks, and other debris (e.g., logs and branches, etc.) that can trap sessile or slow moving animals including hermit crabs (Rocha, 1995; Daniel Gorman, pers. obs.). Trapped individuals that are not freed through subsequent disturbance (or are unable to liberate themselves) face the decision of whether or not to abandon that particular shell to seek a replacement. The time taken for individual hermit crabs to abandon trapped shells, however, will typically reflect holding motivation (Billock & Dunbar, 2009) which will in turn be driven by differences in an individual’s physical state (i.e., condition, energy reserves, size; Houston & McNamara, 1999; Mangel & Stamps, 2001). External environmental factors can also be drivers of motivational change, as demonstrated by the comparatively greater tendency for crabs to abandon small domicile shells in order to approach and investigate newly offered specimens (Elwood & Stewart, 1985; Jackson & Elwood, 1989) and the increased tolerance of higher levels of noxious stimulus when occupying a preferred shell (i.e. electric shocks; Appel & Elwood, 2009b; Elwood & Appel, 2009). Differences in abandonment rate have also been demonstrated in relation to shell adequacy (i.e., 33% more individuals abandon sub-optimal shells than optimal shells) and across differing levels of environmental risk, e.g., abandonment typically occurs within minutes when subjects are buried and face death through asphyxiation vs. hours when they are merely trapped (Turra & Gorman, 2014). It is likely that shell abandoning rates for individuals and species will reflect additional factors linked to shell value, the external environment, and learned behavior (Laidre 2010; Doake & Elwood, 2011).

The aim of this paper was to examine inter-species and context-specific (i.e., for *Pagurus criniticornis*) variation in shell abandoning behavior of hermit crabs under a range of environmental stimuli. We tested the effects of (1) gastropod shell type, (2) shell condition (i.e., damage vs. intact), (3) shell adequacy (i.e., optimum, sub-optimum, and very small), (4) olfactory attractants (i.e., odor of dead gastropods), (5) previous abandoning experience, and (6) shell acclimatization period (i.e., the time allowed to choose an optimal specimen) on the rate at which hermit crabs abandoned trapped shells. These factors were chosen as they represent situations found in the natural environment, and for which there can be positive or negative consequences for the individual. For each experiment, we had a rational prediction as to why there might be differences in the behavior of individuals and treatment groups that related to resource value, attractants, or learned behavior. *P. criniticornis* was selected as the principal test subject because it is a highly active species that has been shown to demonstrate a great tendency to abandon its shell under conditions of simulated disturbance (Turra & Gorman, 2014). All trials tested the hypothesis that there would be no difference among the treatment effects (cumulative proportions) or the abandonment rate (slope over time). The goal of the study was to examine the factors that can influence the expression of a single yet fundamental hermit crab behavior (i.e., abandonment of a key resource that no longer provides substantial benefits).

Materials and methods

Subjects, housing, and simulated entrapment

Although this study centered on the common intertidal hermit crab *P. criniticornis* (Dana 1852) we also examined the responses of two other intertidal species—*Pagurus brevidactylus* (Stimpson 1859) and *Clibanarius antillensis* (Stimpson 1859)—which have a similar reliance on the shells of the gastropod *Cerithium atratum* (Turra & Leite, 2002; Turra & Denadai, 2004). Approximately 650 *P. criniticornis* and 50 *P. brevidactylus* and *C. antillensis* were collected by hand from Araçá Bay, São Sebastião, Brazil (23°48′S, 45°24′W) between May and October. Crabs of a uniform size (3–4 mm shield length) that were collected during periods of low tide were taken to the Laboratory of Aquatic Biology at the Centro Universitário Fundação de Ensino Octávio Bastos where they were housed in marine aquaria under conditions of natural daylight (L12:D12). Aquaria were supplied with controlled temperature (25°C) circulated seawater (salinity, 33–35 psu) that was passed through a glass wool and activated carbon filter (i.e., for bacterial control) with ultraviolet treatment to limit the growth of brown algae. Where 'naked' crabs were required to produce the desired treatments (e.g., for the shell type and adequacy trials), individuals were removed from their shells by gently cracking them using pliers, with only non-injured individuals subjected to experiments.

Experiments were conducted in 10 identical 5-liter plastic basins that were cleaned between trials and supplied with fresh seawater. For each trial, animals were allocated at random to five replicate blocks that were nested within experimental treatment (i.e., 8 animals per basin). Entrapment was simulated by immobilizing 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. Shell attachment was achieved prior to experiments by gluing circular glass disk supports (4 cm diameter) to the top of individual shells. Upon commencement of each experiment, shells were turned upside down so that they were supported by the glass disk and observations were made every 12 h for a period of 5 days following the methods of Turra & Denadai (2004). The metrics used to assess variation in behavioral response were abandonment rate (i.e., change in cumulative proportion over time) and overall tendency for crabs to abandon their shells (i.e., proportions at the end of the trial period).

Inter-specific and sexual variation in shell-abandoning behavior

Turra & Gorman (2014) have previously demonstrated a greater tendency for *P. criniticornis* (an intertidal mud inhabitant) to abandon trapped shells, when compared to *C. antillensis* (rocky areas; Dominciano et al., 2009; Sant'Anna et al., 2012). To further examine the effect of microhabitat occurrence on behavior, we contrasted the abandonment rates of these previously examined species with *P. brevidactylus* which inhabits the mangrove-mud interface. In this way, we provided a test of the relative influence of habitat type (i.e., PB and CA—occupying harder, structurally complex habitats) and phylogenetic relatedness (i.e., PC and PB—shared genus) on the abandonment responses of crabs. Given the variation in predation risk among these microhabitats (see, Gorman et al. in review), we hypothesized that those inhabiting more risky zones (i.e., *C. antillensis*) may demonstrate a greater tendency to retain shells when compared to the two pagurids.

Sexual variation in the preference and ability of hermit crabs to acquire gastropod shells has been demonstrated for a number of species (Asakura, 1995; Gherardi, 2004). To test if there is similar variation in shell abandonment by *P. criniticornis*, we quantified the response of male and female individuals (of a uniform size of 3–4 mm; shield length) to conditions of entrapment. Naked individuals forced to leave their shells were allotted to male and female treatments based on the observations of gonopores. The two treatment groups were then placed in separate aquaria containing a large number of empty *C. atratum* shells ($n > 200$) of varying sizes from which they could select a preferred domicile. Because behavioral variation has been linked to reproductive investments made by females (e.g., egg production and extended parental care; Calado et al., 2006), no berried individuals were included in the trials. It was thus assumed that any behavioral variation would be related to males demonstrating lower risk aversion in a similar way to their greater willingness to undergo agonistic confrontations to gain access to food and shelter (Briffa & Dallaway, 2007).

Gastropod shell type

The effect of shell type was examined by comparing the response of individual *P. criniticornis* inhabiting *C. atratum* shells with those inhabiting *Tegula viridula* shells. The gastropod *C. atratum* produces shells that are elongate (apex–columella axis) which are preferred by *P. criniticornis* under natural conditions (Dominciano et al., 2009). In contrast, *T. viridula* produces shells that have a compressed apex–columella axis which are typically avoided in laboratory trials (Turra & Leite, 2003; Dominciano et al., 2009). It was thus hypothesized that the rate of abandonment would be greater for individuals inhabiting the less suitable shells of *T. viridula*. To produce the desired treatments, eighty naked hermit crabs were allocated at random to two aquaria; the first contained a large assortment of empty *C. atratum* shells ($n > 200$) of varying sizes, while the second contained empty *T. viridula* shells ($n > 200$) of a similar size range. Crabs were held in aquaria until all individuals had taken up residency in a shell (requiring an extended period of 72 h because of the low tendency for animals to take up residency in *T. viridula* shells).

Shell adequacy

The effect of shell adequacy (sensu Vance, 1972) on the abandonment rate of *Pagurus criniticornis* was examined by contrasting the response of individuals inhabiting *C. atratum* shells of an optimal (O), sub-optimal (SO) and very-small (VS) size. Previous work has shown a 33% difference in the proportion of individuals abandoning sub-optimal vs. optimal shells (though both provided some degree of protection to crabs; Turra & Gorman, 2014). It was hypothesized that shells that provide very little protection would elicit a more profound response. Naked crabs allocated at random to the three subgroups were offered a large number of shells ($n > 200$) that conformed to the following characteristics; O = of a size, weight and internal volume ample for the size of the animal; SO = of a limited size (shell length ~1/3 of optimal shells) affording smaller internal volume but still sufficient for the animals to retract their entire body into the shell; and VS = an internal volume too small for subjects to completely retract into and which thus exposed their anterior appendages (see shell adequacy index; Turra, 2003a). Apart from contrasting degree of protection afforded all offered shells were in good physical condition. The preparation of empty gastropod shells along with a validation of the shell adequacy-criteria based on the optimal shell length criterion of Tricarico & Gherardi (2007) were done following the methods of Turra & Gorman (2014).

Shell condition

The effect of shell condition was investigated by comparing the behavior of individuals inhabiting intact and physically damaged shells. Naked crabs were allocated at random to the two treatments, the first offered a large number of intact *C. atratum* shells ($n > 200$) and the second a similar number of physically damaged shells in which the apex and aperture had been broken using pliers (i.e., leaving only the middle section comprising the spire and body whorl; Turra, et al., 2005). While intact shells were of sufficient size and internal volume to enable subjects to completely retract within, damaged shells afforded little protection particularly of the crabs non-sclerotized abdomen. The treatments represent a true test of shell choice under natural conditions as the prevalence and degree of shell damage was similar to that observed in the collection area as a result of shell-breaking predation events (Turra, 2003b; Turra et al., 2005).

Olfactory attractants

Hermit crabs readily attend gastropod predation sites in order to acquire replacement shells (McLean, 1974; Rittschof, 1980; Pezzuti et al., 2002; Turra & Denadai, 2004; Sant'Anna et al., 2012). To test the effect of olfactory attractants that mimic injured or predated gastropods (i.e., and which may infer the availability of a new shell), we exposed one treatment group to the flesh of crushed *C. atratum* ('attractant'), while the other group was maintained under ambient conditions ('no attractant'). Our hypothesis was that individuals might be more readily enticed to leave their existing shells upon expectation of acquiring a newly vacant specimen.

Table 1 Results of Generalized Linear Modeling for variation in the shell abandoning response of the hermit crabs *Pagurus criniticornis*, *Pagurus brevidactylus,* and *C. antillensis* under conditions of simulated entrapment

Treatment	Estimates	Std. error	*t* value	Pr (>|*t*|)
(Intercept)	−1.34	0.27	−4.91	<0.001
time	0.03	0.00	9.33	<0.001
P. brevidactilus	−2.00	0.36	−5.59	<0.001
C. antilensis	−1.67	0.37	−4.50	<0.001
time: (*P. brevidactilus*)	0.01	0.01	2.57	0.011
time: (*C. antilensis*)	−0.01	0.01	−1.72	0.088

Pagurus criniticornis is used as a baseline to enable assessments of which combination of factors (time × species) are significantly different

Previous experience

Hermit crabs demonstrate motivational change in response to previous experience (e.g., memory of potentially painful events, Appel & Elwood, 2009a; recognition of opponents, Gherardi & Atema, 2005; occurrence of food, Thacker, 1996). We hypothesized that individuals rewarded with optimal shells after being forced to abandon their existing shells may demonstrate a greater tendency to repeat this experience. To test this, we compared the rate of shell abandonment of individuals used in previous experiments with those that had been held in the laboratory for the same period of time in their original domicile shells. While we cannot rule out the possibility that some of the 'no experience' individuals had undergone shell abandonment prior to collection, occupied shells were in good physical condition and of an optimal size that inferred little need to have upgraded in the recent past.

Acclimatization period

Given that hermit crabs respond to previous experience (references above) and often invest considerable energy adapting and modifying internal shell architecture (e.g., Laidre, 2012), we hypothesized that the time given to select a preferred shell (i.e., the acclimatization period) may have a bearing on the rates of shell abandonment. To examine this factor, we compared individuals that had been given a prolonged period of time (1 month) in which to select a suitable domicile shell under stable conditions ('long acclimatization') with those that had been given only 2 days ('short acclimatization'). For both treatment groups, individuals were held under identical conditions, with the only difference being that those from the 'short acclimatization' group were forced to select a new shell 2 days prior to the experiment.

Table 2 Results of Generalized Linear Modeling for variation in the shell abandoning response of the hermit crab *Pagurus criniticornis* under various experimental treatments

Treatment	Estimates	Std. error	*t* value	Pr (>|*t*|)
(a) Shell type				
(Intercept)	−3.45	0.72	−4.77	<0.001
Time	0.06	0.01	5.34	<0.001
(b) Shell adequacy				
(Intercept)	−10.63	2.24	−4.74	<0.001
Time	0.15	0.03	4.93	<0.001
Sub optimal	−0.70	0.84	−0.82	0.410
Very small	5.95	1.45	4.10	<0.001
(c) Shell condition				
(Intercept)	−1.55	0.27	−5.75	<0.001
Time	0.03	0.00	9.99	<0.001
Intact	−0.39	0.16	−2.39	0.019
(d) Olfactory attractants				
(Intercept)	−1.88	0.83	−2.26	0.023
Time	0.05	0.01	3.66	<0.001
Attractant	2.13	0.77	2.78	0.005
(e) Previous experience				
(Intercept)	−3.61	1.10	−3.28	<0.001
Time	0.05	0.01	3.62	<0.001
Previous exp.	−4.03	2.85	−1.42	0.157
time: (Previous exp.)	0.12	0.06	1.99	0.047
(f) Period of residency				
(Intercept)	−1.36	0.22	−6.13	<0.001
Time	0.02	0.00	7.90	<0.001
Short occupancy	−0.15	0.28	−0.54	0.593
time: (Short occupancy)	0.02	0.00	5.01	<0.001

The first level of a variable is used as a baseline to enable assessments of which level of a factor (or in the case of an interaction, which combinations) are significantly different

Statistical analysis

The response of hermit crabs to each set of experimental treatments was investigated using generalized linear modeling (GLM) using the lme4 R-package (Bates et al. 2014). Analysis was done on the cumulative proportions of individuals that abandoned shells over time. Binomial GLM has been used successfully for examinations of animal behavior (e.g., Labonne et al., 2003; Cheng & Gallinat, 2004; Cama et al., 2012), including crabs (Chen et al., 2014) and more specifically, decision making in hermit crabs (Briffa et al., 2008a). The main advantage of this approach is that it enables the response to be determined without initial linearizing transformations. The full model included the terms ‘time’ (continuous covariate), respective ‘treatment’ (either 2 or 3 levels), and replicate ‘block’ (included as a random effects term). The model outputs presented (i.e., Tables 1, 2) use the first level of a variable as a baseline (i.e., contribution from the treatment and interaction are 0) to enable assessments of which level of a factor (or in the case of an interaction, which combinations) are different from the baseline (see Zuur et al., 2009). Non-significant terms were dropped from the model using stepwise backward selection until only significant terms remained.

Results

Interspecific and sexual variation in shell abandoning

Pagurus criniticornis responded to simulated entrapment in a markedly different way than did *P. brevidactylus* and *C. antillensis* (Fig. 1a; Table 1). There was a significant ‘time × species’ interaction suggesting that the rate of abandonment for PB will differ from that of PC depending on time (i.e., differing rates of abandonment despite similar cumulative proportions at the end of the experiment), while the rates of CA abandonment will be less than PC irrespective of entrapment time. The cumulative proportion of *P. criniticornis* that abandoned their shells increased rapidly to exceed 60% after just 36 h. This contrasted the lower rates of abandonment seen for the other two species, with *P. brevidactylus* not attaining similar levels until 96 h and *C. antillensis* never exceeding 40% even after 120 h of observation.

There was no difference in the rate of shell abandonment by male and female *Pagurus criniticornis* (Fig. 1b), no differences in the overall tendency (i.e., cumulative proportions at the end of the trial), and only a main effect of time ($P < 0.001$). The overall proportion of crabs that had abandoned their shells at the end of the trial (78% for both sexes pooled) was the lowest observed for any of the experimental trials.

There was no difference in the cumulative proportion of *Pagurus criniticornis* abandoning *C. atratum* or *T. viridula* shells over time (Fig. 2a; Table 2a). The full model revealed no significant interaction between time and shell type and no main effect of shell type; thus these factors were dropped successively from the final model leaving time alone as the best predictor of shell abandoning behavior.

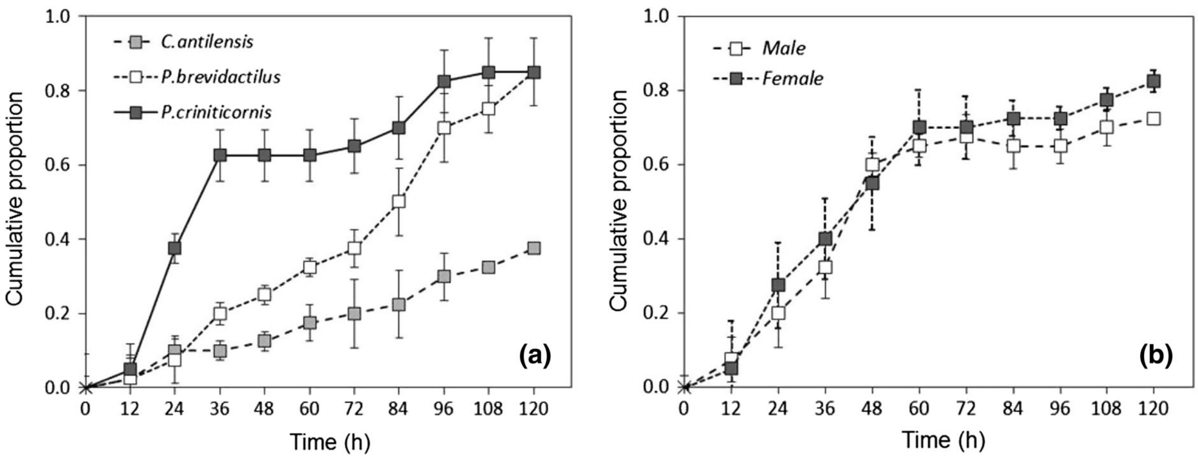

Fig. 1 Variation in the shell abandoning response of **a** three intertidal hermit crabs (*Pagurus criniticornis*, *Pagurus brevidactylus,* and *Clibanarius antillensis*), and **b** male and female *P. criniticornis* under conditions of simulated entrapment recorded over a period of 5 d

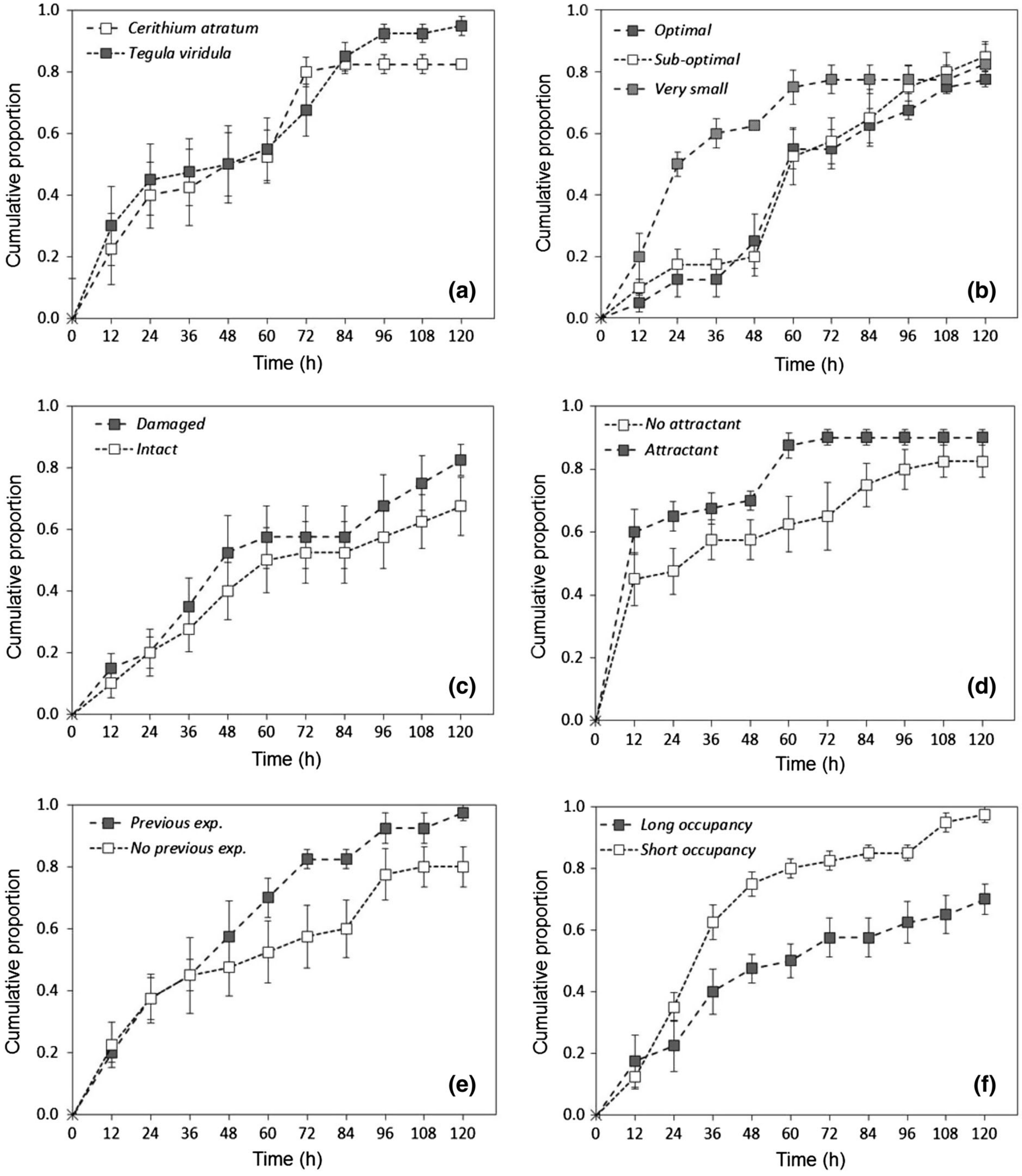

Fig. 2 Variation in the shell abandoning response of *Pagurus criniticornis* under conditions of simulated entrapment across various experimental treatments recorded over a period of 5 d; **a** gastropod shell species, **b** shell adequacy, **c** shell condition, **d** chemical attractants, **e** previous experience, and **f** acclimatization period

There were marked differences in the response of *P. criniticornis* to shells of differing adequacy (optimal, sub-optimal, and very-small) over time (Fig. 2b; Table 2b). The cumulative proportion of individuals that abandoned very small shells reached 60% after 36 h contrasting the slow rates of increase for those in sub-optimal and optimal shells which did not reach similar proportions until 84 h. Although the cumulative proportion of individuals from all treatments was similar at the end of the trial, the abandonment rate suggests that individuals inhabiting very small shells are more sensitive to entrapment. Comparing the proportions of individuals over time, those inhabiting very small shells were 21% more likely to abandon their shells than those inhabiting optimal shells.

There was a significant difference in the cumulative proportion of *P. criniticornis* inhabiting shells of contrasting condition (damaged vs. intact) over time (Fig. 2c; Table 2c). While the model inferred no interaction between treatments, there was a significant effect of time, with individuals inhabiting damaged shells 15% more likely to undergo abandonment than those inhabiting intact shells.

There was a significant difference in the response of *P. criniticornis* exposed to olfactory attractants that mimic gastropod predation sites (i.e., crushed *C. atratum*) and those that were kept under ambient conditions (Fig. 2d; Table 2d). On average, the group exposed to the attractant was 15% more likely to have abandoned their shells than the ambient group, with the greatest differences observed between 24 and 84 h. While the model inferred no interaction between treatments (i.e., no difference in respective abandonment rates over time), it is interesting that the initial rate of increase for the exposure treatment was the highest observed for any of the experimental trials (i.e., exceeding 60% after just 12 h).

Previous abandonment experience had a marked influence on the tendency for *P. criniticornis* to abandon shells when faced with a subsequent entrapment situation (Fig. 2e; Table 2e). The significant interaction inferred that the rate of abandonment over time varied depending on whether individuals had recently been prompted to abandon their shells. While the abandonment rates of the two treatments showed no difference for the first 36 h, they deviated thereafter, so that the group having no experience yielded cumulative proportions ~18% less at the end of the trials.

Variation in acclimatization period yielded the starkest differences in the response of *Pagurus criniticornis* seen for the entire study (Fig. 2f). The significant interaction term (Table 2f) inferred a different rate of abandonment for the group given 1 month to select a preferred domicile shell when compared to those given only 2 days. While the cumulative proportions did not differ for the first 24 h, these deviated substantially thereafter to give a 27% lower likelihood of long acclimatization subjects abandoning their shells than those of short acclimatization.

Discussion

This study highlights variation in the behavior of three species of intertidal hermit crabs in response to a trapped shell. *P. criniticornis* rapidly abandoned shells with >60% of individuals electing this strategy within the first 36 h, and the remainder (cumulative total of 85%) doing so within 5 d. This species dominates the intertidal mud/sand zone of Araçá Bay (Sant'Anna et al., 2012) where disturbance is frequent but predation risk can be low (Gorman et al., In review). *P. brevidactylus* exhibited a similar overall response, albeit at a slower rate, which might reflect the higher risks of predation at the mangrove-mud interface where this species is found in high abundance (Leite et al., 1998; Turra et al., 2000; Sant'Anna et al., 2012). The behavior of the two pagurids contrast that of *C. antillensis* which displayed a low tendency to abandon that did not exceed 40%. *C. antillensis* occupies rock and boulder strewn substrates (Turra et al., 2000) where predation can be high due to the inability of crabs to burrow (Turra & Denadai, 2003). This increased risk may motivate trapped *C. antillensis* to hold shells for a longer period of time which may increase the likelihood of subsequent dislodgement. The competing strategies appear to reflect optimal behaviors that balance the competing demands and risks of microhabitat distributions, e.g., in highly variable mud environments characterized by low predation, the optimal strategy is to rapidly seek a new shell that will not limit nutrition and reproduction, while in a high predation environment the risks of abandonment warrant holding a shell resource.

Focusing attention on *P. criniticornis*, we see that the greatest rates of abandonment occurred within the first 48 h, reflecting the high activity and exploratory nature of this species (Turra & Denadai, 2003, 2004). Despite this tendency (i.e., which was consistent across sex and all of the factors tested), there was still considerable variation in the response of individuals (i.e., mean ~15% of subjects remained in their shells after 5 days) which may reflect personality (see Briffa et al., 2008b) or differences in physiological state (i.e., condition, energy reserves, and size). Differing responses may be expressed across different environmental contexts, e.g., variations in the shell abandoning or startle response of hermit species under different levels of risk (Briffa, 2013; Turra & Gorman, 2014), and this may be better understood by examining the importance of shell quality, cues that infer new shell resources, and previous experience. Our results suggest that the tendency to abandon shells relates to their perceived value (i.e., small and damaged shells are abandoned rapidly), the anticipation of acquiring a replacement (i.e., the dramatic response to gastropod predation cues), acclimatization period (i.e., which presumably allows selection of the best available specimens), and previous experience (i.e., successful upgrades may increase the tendency to repeat this response). These factors appear to moderate the response of *P. criniticornis*, the response to which is likely to form a suite of correlated traits that have evolved to enable this species to exploit its intertidal habitat (see, Sih et al., 2004). The present distribution of *P. criniticornis* is probably an outcome of spatial and temporal variation in species interactions (Agrawal, 2001) and its strategy of rapidly abandoning shells may be an expression of behavioral plasticity that optimizes tradeoffs in order to make 'the best of a bad situation' (e.g., Gherardi, 1996; Rodrigues et al., 2002).

Shell abandoning in the context of resource value

Given that hermit crabs assess shell value based on internal volume and hence the protection afforded (i.e., an attribute defined as adequacy; Vance, 1972; Turra, 2003a; Turra & Gorman, 2014) the absence of a disparate response between crabs inhabiting different gastropod shells is surprising. The morphologies of the two gastropod shells (i.e., *C. atratum*—elongate apex-columella axis vs. *T. viridula*—compressed apex-columella axis) would surmise that the former provides greater protection from predators since crabs are able to fully retract inside. Although hermit crabs often exhibit fidelity to particular shell morphologies, e.g., *P. criniticornis* strongly favoring *C. atratum* during shell selection trials (Dominciano et al., 2009), this does not appear to convey to any greater tendency to abandon less preferred shells (but see Elwood & Appel, 2009). While *T. viridula* shells may not be optimal, they might provide sufficient levels of protection that once an individual has taken up residency, there is little incentive to relinquish this resource given the predation risk and the uncertainty of acquiring a replacement (Fotheringham, 1976). Recent tethering experiments involving these two shell types have also shown that while rates of *T. viridula* abandonment in nature may be higher, predation risk may actually be lower as predators tend to overlook these shells as targets (Gorman et al., In review; Turra et al., 2005).

Shell adequacy determines the amount of time a hermit crab will attempt to hold a particular shell (Rotjan et al., 2004) because it has implications for growth potential and predation susceptibility (Angel, 2000). In recent laboratory studies, *Pagurus criniticornis* occupying sub-optimal shells showed rates of abandonment that were 33% greater than those in optimal shells (Turra & Gorman, 2014). Similarly, the tendency for *Pagurus bernhardus* to approach, investigate, and enter newly offered shells has been shown to relate to existing domicile shell size (Elwood & Stewart, 1985; Jackson & Elwood, 1989). The present study extends the findings for *P. criniticornis*, showing a greater tendency to abandon very small shells (>60%) compared to optimal and sub-optimal specimens (both <18%). Such high rates of abandonment attest to the low value of very-small shells, even when compared to undesirable shells from other gastropod species (cf. results of gastropod shell type experiment). For hermit crabs, a prolonged decision time has been equated with a low motivation to acquire a resource (Billock & Dunbar, 2009). Conversely, the slow rates of abandonment seen for optimal and sub-optimal shells in our trials may suggest greater motivation to hold these existing resources. Turra & Gorman (2014) showed that hermit crabs will almost unanimously abandon even high-value shells if there is a serious risk of injury or death, i.e., through burial and subsequent asphyxiation. The risk of predation imposed by a very small shell appears to elicit a similar response, prompting individuals to abandon such shells in search of a more suitable replacement.

Shell condition is another factor that directly influences predation risk (Bulinski, 2007) and consequently the time an individual hermit will remain in a shell (Rotjan et al., 2004). Our results show that individuals inhabiting damaged shells abandoned them more rapidly and in greater numbers than those in intact shells (i.e., 13% more after 5 days). A damaged shell is likely to provide less protection and therefore substantially increase the risk of predation (McClintock, 1985; Angel, 2000). While a very small or sub-optimal shell may expose a crab's anterior appendages to injury, one that is physically damaged (particularly if the apex is broken) poses a greater risk as it exposes the crab's non-sclerotized abdomen. Recent field experiments involving tethered *P. criniticornis* have shown that rates of predation and abandonment are considerably greater for damaged shells (22 and 53%, respectively; Gorman et al., unpub. data). While most species of hermit crabs are able to contend with damaged or perforated shells (for want of a better one; Taylor, 1981), the majority of individuals avoid heavily damaged shells if given a choice (e.g., *Pagurus longicarpus*; Pechenik & Lewis, 2000), and our study shows that they readily abandon such shells to seek replacements that provide greater protection.

Shell abandoning in response to olfactory cues

The scarcity of empty shells in many estuarine and coastal habitats (Fotheringham, 1976) means that replacements are often sourced through exchanges (Chase et al., 1988) or by encountering gastropods that are dead or injured (Rittschof, 1980). McLean (1974) made the first observations of chemical signals associated with hermit crab attendance at gastropod predation sites (i.e., where predator gastropods prey on other gastropod species). Crabs are attracted to such sites by olfactory cues derived from gastropod flesh (Rittschof, 1980; Katz & Rittschof, 1993; Pezzuti et al., 2002) with the intensity of attraction believed to be governed by behavioral plasticity modulated by crab size and the type of preferred shell (i.e., relating to adequacy and physical condition; Gilchrist & Abele, 1984). Our results show that *P. criniticornis* exposed to crushed *C. atratum* display a greater tendency to abandon their shells than those kept under ambient (non-exposure) conditions. Crabs appear more willing to risk abandonment when they detect such cues, presumably in anticipation of a new high-quality shell that may afford greater comfort and protection. Because gastropod predation sites may be one of the best markets from which to obtain a new shell (Rittschof, 1980; Pezzuti et al., 2002), such cues should be expected to elicit a rapid and pronounced response. Indeed, the rate of abandonment for crabs exposed to gastropod flesh was the greatest of all the experiments (i.e. >60% of exposed individuals within 12 h). The allure of a new shell may help to explain why individuals inhabiting small and inadequate shells (i.e., urgently requiring an upgrade) respond more rapidly to gastropod predation cues than large individuals carrying adequate shells (Pezzuti et al., 2002).

Shell abandoning in the context of learned behavior

Hermit crabs demonstrate learned behavior (Gherardi & Atema, 2005; Laidre, 2010; Elwood, 2011) which is likely to be reflected in the willingness of individuals to abandon trapped shells. We show that crabs previously experiencing shell abandonment (earlier trials) exhibit a greater tendency to repeat this response (~ 98%) than those which had not undergone this experience and retained the shells in which they were collected (80%). Similar reproducible behaviors have been demonstrated in relation to shell acquisition over short periods of time (after just 30 min; Katz & Rittschof, 1993) and it is possible that individuals rewarded with optimal replacements may be more willing to risk shell abandonment. The concept of learned behavior in hermit crabs is further backed by the results of the acclimatization experiment. Here crabs that were allowed a longer period in which to choose (and possibly compete for) a suitable shell (i.e. 1 month) were 28% less likely to abandon their shells than those given only 2 days. Indeed, this factor accounted for the greatest difference among treatments observed for the entire study. The results imply that once a hermit has selected its preferred domicile shell from those on offer (i.e., an issue of subjective resource value; Turra & Gorman, 2014), it may be less willing to risk abandonment given the uncertainty of finding a quality replacement (Fotheringham, 1976).

In conclusion, we show that shell entrapment can motivate common intertidal hermit crabs to abandon their shells in a way similar to losing a competitive interaction (Dowds & Elwood, 1983), experiencing adverse stimulus (Elwood & Appel, 2009) or encountering a superior replacement (Elwood & Stewart, 1985; Jackson & Elwood, 1989). The speed of the response however varies among species, an observation that is likely to reflect different optimal behaviors suited to their respective intertidal distributions (see, Sih et al., 2004). For *P. criniticornis*, the behavior appears to be modulated by shell attributes (i.e., those that minimize predation risk), olfactory cues (i.e. those indicative of new shell resources), and previous experience (those that balance risk vs. reward). Our findings are likely to enhance understanding of how hermit crabs may respond to changing environmental conditions (see similar studies on water chemistry and contaminants; de la Haye et al., 2011; White et al., 2013). Perhaps more importantly, evaluating how various factors affect the behavior of hermit crabs may aid our understanding of behavioral plasticity and consistency in not only invertebrates but potentially other marine animals that rely on refuges (e.g., bivalves in sediments; Skilleter & Peterson, 1994; echinoderms in crevices; Drolet et al., 2004; and fish within submerged aquatic vegetation; Laegdsgaard & Johnson, 2001) and to a greater degree those that are obliged to upgrade shelters throughout their lifetime (e.g. urchins; Scheibling & Hamm, 1991). Examining animal behavior in the context of ecologically and evolutionarily important trade-offs is vital for intertidal and subtidal research given a current lack of basic quantitative natural history for most taxa. Given that countless aquatic species rely on refuges and/or ephemeral habitat patches, understanding when and how animals choose to relinquish these resources is an important ecological question worthy of further research.

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