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# A comparative study of aggression and spatial differences between two populations of *Pagurus bernhardus*

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Hermit crab populations are limited by shell availability; therefore fights to gain a suitable shell are frequent. Although a large amount of research has studied hermit crab aggressive behavior, few have correlated this behavior with location. This study was carried out to investigate the influence of wave exposure on the behavior of the common hermit crab *Pagarus bernhardus*. Crabs from two sites on Isle of Cumbrae, with differing levels of wave exposure, were tested for their aggressive behavior in laboratory trails. Our results showed no significant difference ($p > 0.05$) in overall behavior between de-shelled crabs from sheltered sites and those from exposed areas. However, when the behaviors were considered independently, fighting did show significant differences ($p < 0.05$), possibly due to *P.bernhardus* from exposed sites being more aggressive. This behavior was altered when the crabs from each location retained their shells, resulting in no significant difference in overall behavior and fighting behavior ($p > 0.05$ and $p > 0.05$ respectively). This suggested that *P.bernhardus* is more aggressive in stressful situations (without shell protection) and this behavior is masked under normal conditions. Predator presence (*Necora purer*) had no significant effect on the shell search time of de-shelled hermit crabs.

## INTRODUCTION

The common hermit crab, *Pagarus bernhardus,* is a species of marine crustacean that is highly abundant in the coastal waters of the north Atlantic (Fernandez-Leborand and Gabilondo 2005). Hermit crabs lack calcification of the abdomen (Doake et al. 2010) so they utilize gastropod shells for protection (Nakin and Somers 2007). Like all species of hermit crab, *P.bernhardus* has the unique ability to choose an external housing for its vulnerable abdomen, typically by occupying the shells of deceased gastropods such as the Periwinkle, *Littorina littorea* and the Dog whelk, *Nucella lapillus* (Briffa and Elwood 2005). Once entered by the crab, the shells provide invaluable protection from predators (Barnes 2003) and environmental stress (Reese 1969). An optimum sized shell is one where the crab can withdraw completely and block the shell aperture with its chelipeds to prevent predation or eviction (Ismail 2010). Occupying shells that are too small can increase haemolymph lactate levels due to restricted water flow over the gills, decrease fecundity and limit growth (Doake et al. 2010). Most hermit crab populations are limited by shell availability or shell quality (Fotheringham 1973) resulting in high levels of intra-specific competition. The major sources of new or larger shells are those already occupied (Scully 1983). Naturally, this competition for optimal shells will result in fighting between individual crabs.

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The probability that one crab will approach another depends both on the properties of its own shell and that of its opponent (Elwood and Stewart 1985), with crabs occupying significantly sub-optimal shells more likely to approach (Hazlett 1970). After the initial approach a crab will “size up” its opponent by rapping its cheliped against its shell (Briffa *et al,* 1998) and if the fight is deemed worthy of the vulnerability and energetic cost (Doake et al. 2010) the attacker will attempt to oust the defender from its shell, either by physically removing it or by causing it to flee its shell (Elwood and Glass 1981). Very similar mechanisms are also present in the case of predator attack such as by the common shore crab *Carcinus maenas*, with *P.bernhardus* always being the defender and withdrawing fully into its shell in response to the perception of an attacking predator (Vance 1972).

This paper focuses on whether exposed populations of crabs are more aggressive than sheltered

## MATERIALS AND METHODS

### Site Location and Resource Availability

Two sites were selected on the Isle of Cumbrae (55.752°N, 4.930°W), one exposed and one sheltered (Fig. 1). These were characterized on resource availability and the seaweed community present. Site A (Fig. 1b), a rocky bay just outside the town of Millport (grid reference NS 1584 5449) was classified as a sheltered site due to its large number of relatively deep rock pools which were kept calm and sheltered from the waves by large rock formations. Site B (Fig. 1c)(Grid reference NS18055503) was classified as exposed as it contained a larger number of rock pools but was much more exposed to hydrostatic and wind pressure due to its geographic location on a straight piece of coast line with few large rocks.
Available resources were assessed by randomly placing n = 50, 1 m² quadrants at each site and counting the number of empty

dogwhelks, N. lapillus, and periwinkles, L. littorea and the number of crabs in each type of shell.

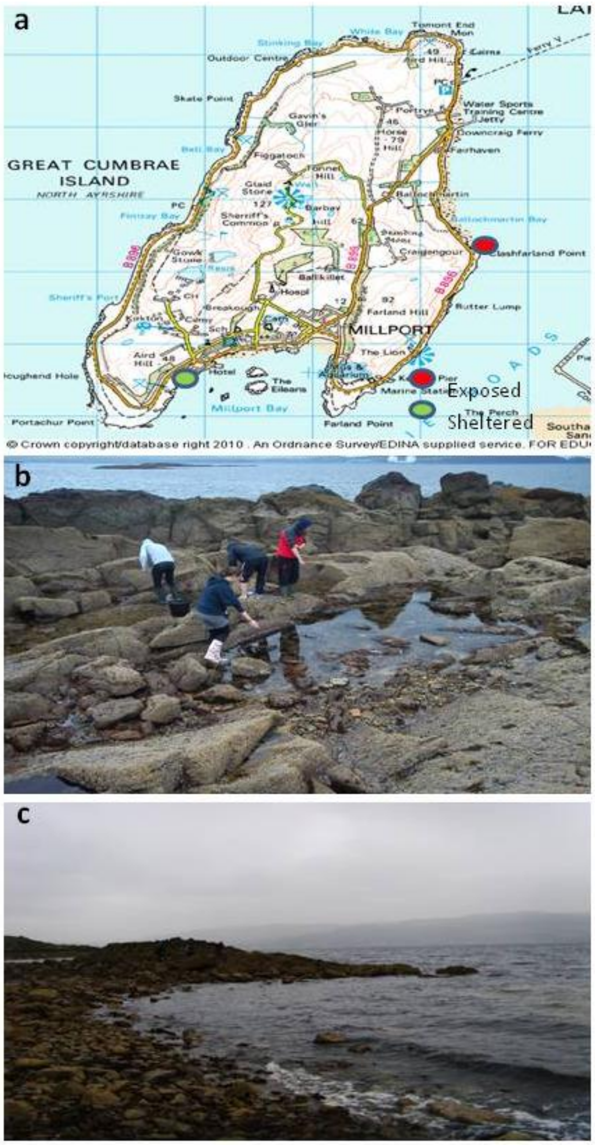


**Figure 1**: Location of P.bernhardus used in experiments; (a) Map of Isle of Cumbrae with sheltered (dark green) and exposed (red) sites (b) picture of sheltered site (c) picture of exposed site

## De-shelled aggression experiment

N=120 crabs were collected from each location. The crabs were sorted by shell size: small <14.9mm, medium 15-18.9mm, and large >19mm. Shells were measured with calipers from the spire to the bottom of the aperture. Medium sized crabs (15-18.9mm) were used in all experiments. Shells were gently removed using a vice ensuring that no injury was caused to the crab as in previous studies (Absher et al. 2001; Pechenik et al. 2001). The crabs were then left to habituate for 10mins before use in the trial. Two de-shelled hermit crabs were placed in a seawater aquarium equidistant from an optimal shell to remove the influence of other factors such as variations in proximity to the shell. Each trial was designated to run for 10 mins as during preliminary trials aggressive encounters occurred within the first few minutes. This is concurrent with other experiments such as (Gherardi 2006). During each trial, specific behaviors were recorded: time to enter shell, confrontation, fighting, rapping, attempted swapping, swapping and no interaction. Crabs were identified by differences in color or tracing their movements around the tank. Used crabs were placed in separate tanks to avoid reuse and acquired behavior (Biagi et al. 2006). A total of 40 trials of each of the following categories were performed; exposed vs. exposed, exposed vs. sheltered and sheltered vs. sheltered. Crabs were kept in aerated seawater with seaweed when not in use.

| Species | Common Name | Present at exposed | Sheltered |
|---|---|---|---|
| *Ascophyllum nodosum* | Egg Wrack | X | |
| *Ahnfeltia plicata* | BlackScour Weed | X | |
| *Chrondrus crispus* | Irish Moss | X | |
| Cladophora rupestris | Common Green Branched Weed | X | X |
| Comsothamnion thuyoide | | | X |
| Crytopleura romosa | Sea Beach | X | |
| Dictyota dictoma | Common Forked Tongue | X | X |
| Fucus cerandoides | Horned Wrack | | X |
| Fucus serratus | Toothed Wrack | | X |
| Fucus spiralis | Spiral Wrack | X | X |
| Fucus vesiculosus | Bladder Wrack | X | X |
| Halidrys sliliquosa | Sea Oak | | X |
| Jania rubens | Slender-beaded Coral Weed | | X |
| Laminaria digitata | Oarweed | X | |
| Laminaria saccharina | Sea Belt | X | X |
| Lomentaria articulata | Bunny Ears | | X |
| Mastocarpus stellatus | Carragheen | X | |
| Pelvetia canaliculata | Channelled Wrack | X | X |
| Saccharina latissima | Sugar kelp | X | |
| Sccorhiza polyschides | Furbelow | X | |
| Sargassum muticum | Siphon Weed | X | |
| Spirogyra spp | Mermaid Tresses | | X |
| Spongomorpha sp. | Spongy Weed | X | |
| Ulva lactuca | Sea lettuce | X | |
| Various | Corline Algae | X | |
| Total | | 18 | 13 |

**Table 1**: Seaweed species present at sheltered and exposed site. Presence indicated by 'X'.

## Shelled Aggression Experiment

Journal of Young Investigators RESEARCH ARTICLE

This experiment was essentially a variation of the de-shelled aggression trial. A total of 60 crabs from the exposed and sheltered location were collected. A shelled exposed and shelled sheltered crab; were placed in aquaria with seawater and the

### Predator Interaction Experiment

A de-shelled sheltered and a de-shelled exposed crab were placed in a glass tank containing seawater, an empty periwinkle shell, and a predator , the Velvet Swimming Crab, Necora puber. Time until a hermit crab entered the shell and identity of hermit crab were recorded. There were 30 trials lasting 10 min. Control experiments had no predator present.

### Statistical Analysis

All statistical analysis was carried out using the statistical software Minitab. Statistical methods used were One-way ANOVA, Two-way Chi-Squared and graphical representations of data were constructed using Microsoft Excel.

## RESULTS

### Site Selection and Surveying

Site selection was based on the seaweed community present as Blamey and Branch (2009) found that there was greater species richness at exposed shores and so the basis of species richness was used to distinguish between sheltered and exposed sites. There were 18 species of seaweed at the exposed site compared to 13 species at the sheltered site, (Table 1), including species which grow exclusively at exposed areas of coast such as Sargassum sp., Ascophyllum nodosum and Saccharina latissima (Wernberg and Connell 2008).

There was a significant difference in the availability of shells between the exposed and sheltered site (p = 0.001). There was a greater number of both species of gastropod shell L. Littorea (557 and 111) and N. lapillus, (86 and 46) respectively at the sheltered site then at the exposed site (p = 0.0001; Fig. 2). In addition a significantly higher number of periwinkle shells were found at both sites in comparison to dog whelks (557 compared to 86 at the sheltered site

### De-shelled Aggression Experiment

There was no significant difference (p = 0.231) in the overall behavior between hermit crabs from the sheltered and exposed sites. However, by separating behavior categories, we found a significant difference (p = 0.001) in fighting between the sheltered and exposed crabs. There was no significant difference between other behaviors: attempted swap (p = 0.094), swapping shells (p = 0.157), confrontation (p = 0.544). There was a slight difference in the occurrence of the different behavior categories (Fig. 3a), suggesting there could be a real difference but further work is needed.

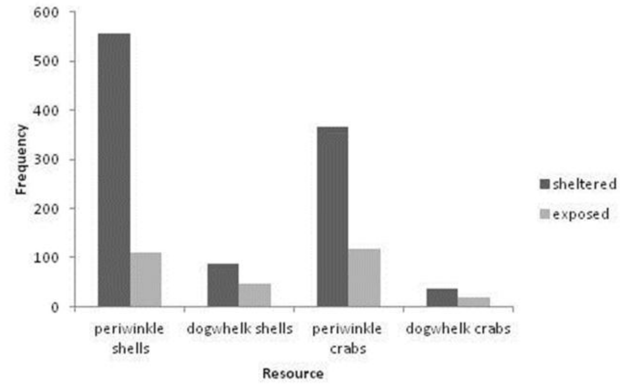


**Figure 2**: Graph showing the results of the quadrat survey. On the X axis "shells" denotes empty shells and "crabs" denotes a shell of that species, with a crab living inside it. A greater number of both types of shell, occupied and unoccupied, were found at the sheltered site. A significantly higher number of periwinkle shells were also found at both sites compared to dog whelks.

### Shelled Aggression Experiment

No significant difference was found overall (p = 0.974) suggesting crabs do not waste energy fighting unnecessarily. Exposed P.bernhardus exhibited slightly higher frequencies of rapping and swapping, and fighting compared to sheltered crabs suggesting that there may be a real difference as there is a difference in frequency, however further trials are needed to determine if there is a significant statistical difference (Fig. 3b). Similarly, exposed crabs showed a lower frequency of 'no interaction' to sheltered (0.71 and 0.9 times per trial on average respectively), suggesting they are more aggressive. All other behaviors were observed at the same frequency, with the exception of 'retreat', which was more frequent in the exposed crabs.

### Predator Interactions

When the predator was absent, there was no significant difference (p = 0.996) in the search time to discover and enter the shell between the sheltered and exposed crabs. Therefore, in order to determine if there was a difference between the search times of when a predator was present and absent, the two locations were grouped. No significant difference occurred in time taken for a crab to get in a shell when a predator was present (p = 0.868). The exposed crab occupied the shell in 70% of trials. As there were few swaps, this may support the findings that exposed crabs are more aggressive than sheltered or they explore their surroundings more than sheltered crabs.

## DISCUSSION

In shell limited populations, fighting is frequent because of a high probability of finding an animal in a better shell whereas in populations where resources are not limited, fighting occurs less often as it's less costly to investigate empty shells (Scully 1983). As there was no difference in aggression between the sexes, (Absher et al. 2001) sex could be removed as a factor governing aggressive behavior. It may also be possible that crabs from crowded habitats tolerate other crabs coming closer before becoming aggressive compared to hermit crabs from sparsely populated areas (Lancaster 1988). A significant difference in aggression was found between sheltered and exposed crabs only when the recorded behaviors were considered separately, where exposed crabs were found to fight more often. As the sheltered site has a higher population density of hermit crabs then the exposed site, this may be a further factor explaining the difference of aggression between the two populations. Out of 120 trials, there were 16 successful evictions of the crab occupying the shell. This reflects findings by Abrams (1987) and Pechenik et al. (2001) who with comparable sample sizes found that the occupying crab usually retains the shell and <50% of evictions are successful.

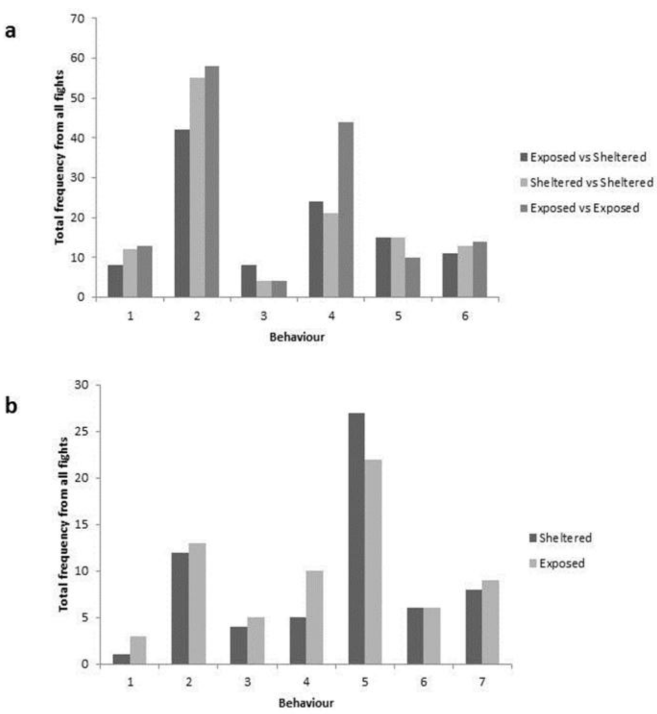


**Figure 3:** Graph showing the average frequency of the occurrence of the behaviors observed in P.bernhardus in the naked aggression trials; (a) De-shelled aggression trials (b) shelled aggression trials. (1=Rapping; 2= Confrontations; 3= Swapping; 4= Fighting; 5= No interaction; 6= Attempted swapping; 7=Retreat).

Motivation plays an important part in fights (Briffa and Sneddon 2007) and de-shelled hermit crabs were highly motivated to gain the protective shell. This may explain why in the shelled trials the instances of no interaction increased. Absher et al. (2001) findings agree with the results in this study, whereby de-shelled hermit crabs are more aggressive than shelled. As both crabs were in the shells they were found in, it can be assumed that these are optimum shells so there was minimal motivation to fight. When hermit crabs are more vulnerable (i.e. an exposed abdomen) they are less selective of a new shell (Ismail 2010). Therefore, the fact that the P.berhardus were cracked out of their shells may have increased aggression in the search for a new shell; similarly, it has been shown that de-shelled crabs use their minor cheliped for investigation, saving the larger cheliped (used by housed crabs for investigation) for defense (Elwood and Stewart 1985). Because of this, the results may not be an accurate representation of behavior in the wild. Elwood and Glass (1981) carried out a similar de-shelled crab's experiment which found evidence for the aggression model and also the outcome of an encounter being determined by the larger crab, so the fact that all the crabs in this study were of the same size may increase the reliability of any differences between the two sites. However, it is important to note that when looking at some of the behaviors individually (e.g. fighting and confrontation) a significant difference was found between the two sites. Therefore, these results suggest that aggression can be influenced by habitat, especially as fighting and confrontations are strong indicators of aggression. The individual behaviors can be seen to follow a repeatable pattern, with a certain amount of time being spent on each before the crab moves onto the next. The fact that each of the behaviors was observed in every set of trials is evidence that they are all important in shell competition and is an example of the complexity of this behavior that is unique to hermit crabs (Briffa and Elwood 2005). It is possible that exposure can influence these patterns causing those that are linked to physical aggression more closely being repeated at a greater frequency or for a greater duration of time in contrast to behavior that are linked less strongly to actual combat (e.g. rapping and attempted swapping).

Rapping is defined by Doake and Elwood (2011) as an "assessment of a potential shell", but this is not necessarily an indication of aggression as hermit crabs are always open to moving to better suited shells (Elwood and Jackson 1988) .When studying the behaviors individually it would be logical to assume that shell assessment would not differ between crabs from contrasting sites. They are using shells from the same source and are in equal need of a new shell and thus no significant difference would be expected which was reflected in our results. Whereas for behaviors that involve interacting with a rival, such as fighting, a significant difference was observed due to the fact that the specimens are encountering the behavior cycles of rivals.

In other organisms, for example the lobster Homarus americanus, aggression varies throughout the moulting cycle (Scully 1983). As hermit crabs have a vulnerable soft exoskeleton for a few days after a moult (Hazlett 1969), it is possible that this factor could influence levels of aggression in hermit crabs, therefore aggression would be expected to vary throughout the lifecycle. As only the accessible part of the population in the intertidal zone was considered, there may be different aggression levels within the subtidal population and further trials should be conducted with this in mind.

No significant difference in the predator trials suggests evidence against alerting olfactory or visual cues from the predator N. puber. This could be explained by the fact that as P.bernhardus is usually protected by its shell and has a small chance of fighting off a large predator; it is less energetically costly to move away from the predator so it instead simply withdraws into its shell (Briffa et al. 2008). However, other factors, such as the unnatural environment of the laboratory, should not be excluded and could potentially cause an element of stress on test animals altering natural behavior.

Future research could focus on conducting trails in the wild to investigate if the laboratory has an effect on the crabs' behavior. In a broader context different locations and habitats, including different intertidal zones, could be studied. Similarly other species of hermit crab that exhibit similar behavior could be observed to further investigate differences in aggression based on wave exposure.

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