Consequences of shell choice in diogenid hermit crabs from Queensland, Australia.

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Abstract

Shell selection is an important determinant of survival and possibly reproductive success amongst the hermit crabs, Paguroidea. The evolution of hermit crabs is closely tied with that of gastropods and hence it is reasonable to suggest a selective pressure for an ability to assess and choose an optimal shell. Three species of diogenid paguroids were collected from Heron Island, Queensland Australia. Hermit crabs were turned aperture upwards and the time taken to emerge and fully right itself were recorded. *Dardanus megistos* was more efficient than the other two species when righting itself and there was some evidence that the different species were utilising different shells. *Strombus luhuans*, the red-lipped stromb and *Trochus* shells were the most commonly collected shells with hermit crab occupants. Both the emergence and righting performance was significantly higher in strombs than *Trochus*, though *Trochus* shells are very heavy relative to size and are proposed to offer the greatest protection from predators amongst the shells considered. Whether or not shell occupation frequencies simply reflect availability within the environment, the consequences of shell choice remain real. Certainly different shells can be considered to influence performance and fitness along multiple measures and it is likely that shell choice, via predation, is one of the strongest selective pressures on hermit crabs.

Introduction

Hermit crabs are a diverse (McLaughlin *et al.* 2010) and well known group. Their dependence on a gastropod shell for protection has made them the focus of many behavioural and optimality studies (Briffa and Elwood 2005). It is now well established, that at least some, if not all hermit crabs, have the capacity to discern between gastropod shells and assess their suitability (Mantelattoand de Lucca Meireles 2004). Regardless of whether

Previous studies have focused on the relative body size between crab and shell (Mantelattoand de Lucca Meireles 2004), internal volume (Mantelattoand de Lucca Meireles 2004) and the presence of an epibiotic community, thus the degree of crypticism (Briffa and Elwood 2005). Obvious shell preferences are not, however, always present. Reece (1962) found no evidence in differences in shell preference between sexes or across populations of pagurid hermit crabs. Though differences may be apparent between species (Reece 1962)

This study aims not to investigate determining factors of shell selection but instead the consequences of shell choice. This aim is therefore relevant regardless of whether hermit crab occupancies simply reflect gastropod shell abundance patterns or are the result of active decision making. Three species of diogenid hermit crabs from the Great Barrier Reef are considered, a region under-represented for literature on Paguroids.

Methods

Data Collection

Hermit crabs were collected from the reef flat, reef crest and sandy inner reef zones of Heron Island, Queensland, Australia, across a week in September 2012. Crabs were maintained in aquaria with flowing sea water for the duration of the study and all were returned unharmed to the reef flat.

The host shell of each subject was identified to species level or the lowest taxonomic rank possible given shell condition. Shells were further grouped by shape based on Wilson (2002). Gross weight of shells with crab (water drained) was recorded and standard length/width shell measurements taken as per Wilson (2002).

Performance trials were conducted in a separate container to the holding tank to avoid the influence of conspecifics. Because the focal species are marine, hermit crabs were submerged for all trials. Initially crabs were placed in a plastic tray though a layer of sand/shell grit from the field was added later as it was noticed that some crabs suffered extra difficulty righting on a uniform surface, a problem not characteristic of a hermit crab's normal habitat. All trials were conducted under consistent fluorescent lighting.

Shells were turned aperture upwards and crabs were encouraged to fully retreat into the shell. The elapsed time taken first emerge from the shell and second to fully right itself was recorded. Emergence was defined by a repeatable behaviour where the crab would pause, either momentarily or for a longer period, as it reached the aperture, eyestalks fully extended. The time taken to right itself was measured not from the start of the trial but from when the crab first began to attempt the movement. Again this was readily distinguishable. The crab reached down with its chelipeds, second and third periopods extended, exposing the shield and then pereon.

Data Analysis

In many cases a hermit crab would not emerge for long periods, sometimes several hours, or similarly would emerge but make no attempt to right itself. Considering time constraints of the project, such crabs were sometimes left for several hours while other trials run, or the trial was abandoned. This resulted in many null data values. Removal of this information however is not justified, as the study is interested in the time taken by Paguroids to right themself. Similarly, because the measurement of interest was elapsed time, a value of zero could not be recorded for these trials, this would reflect the fastest possible response, rather than the slowest.

To overcome the problem of null values without loss of information, elapsed time measures were converted to scores. This adjustment was ad-hoc, but is justifiable given the circumstances. Initially it was considered most simplistic to subtract each value of both emergence and righted elapsed times from the corresponding maximum of those trials that did record a value. Thereby rather than counting elapsed time, effectively a countdown was started for each trial. Crabs failing to emerge or right themselves within the countdown period would therefore receive a score of zero, while the fastest crabs would score most highly.

This strategy however had two problems. Firstly, the slowest crab recorded, that is, the crab with the maximum elapsed time for which the scoring system is based, will always receive a score of zero, equal to that of crabs that didn't right themselves at all. More importantly this strategy lacks standardisation and is bias. It is likely that the maximum elapsed time was recorded from a subject measured early in the study period, when the observer was certain to be more patient before abandoning a trial. Therefore some crabs recording a null measurement might actually have righted themselves sooner than the maximum recorded, if given the chance.

To overcome these problems, trials without null values were separated and the interquartile (quartile 3 – quartile 1) range was calculated for both response measures. These values were multiplied by a factor of 1.5 and added to quartile three, as per the standard 1.5xIQR rule for detection of outliers. This value now became the cut-off, if crabs could not right themselves within this period they were assigned a score of zero, regardless of whether they had been observed to right themselves at all.

As response measures were not normally distributed, nonparametric, unpaired pairwise Mann-Whitney tests without a p value adjustment correction were performed to compare the Paguroid species and their choice of host, both species and shell type. All statistical analysis was carried out in the free software R.

Results

In total, 27 individual diogenid hermit crabs were collected; 6 of *Calcinus gaimardii*, 5 of *Dardanus megistos* and the remainder *D. lagopodes*. *Calcinus gaimardii* was significantly smaller than the other two species (p val < 0.01), which were similar in size. *D. megistos* however can reach substantially larger sizes, reportedly up to 30cm. One such large individual was collected in this study, from a baler shell, *Melo amphora*, with a gross weight of 1 019 grams.

A Chi-squared test suggested differential usage of shell forms by the three species (p = 0.0553) but this was not detectable at the gastropod species level. The obconical red-lipped stromb, *Strombus luhuans,* was the most commonly utilised shell and from field observation alone it appears to be the most common gastropod of this size class in the sandy inner reef at Heron Island. The only other shell considered obconical was the textile cone, *Conus textile*, occupied by both *Dardanus* species. Aside from the *Melo amphora* and a spider conch, *Lambis lambis* (*D. dardanus*), the textile cones recorded the heaviest gross weights along with the single sand creeper (*Cerithium nodulosom*) and the five *Trochus hanleyanus*, all occupied by *D. dardanus* (Figure 1). These latter two species were however heaviest relative to shell dimensions. The thinner *Conus textile* shells were simply larger and also happened to have larger crabs within them. The obconical (*Conus, Strombus*) and conical (*Trochus*), were the most commonly utilised shell form.

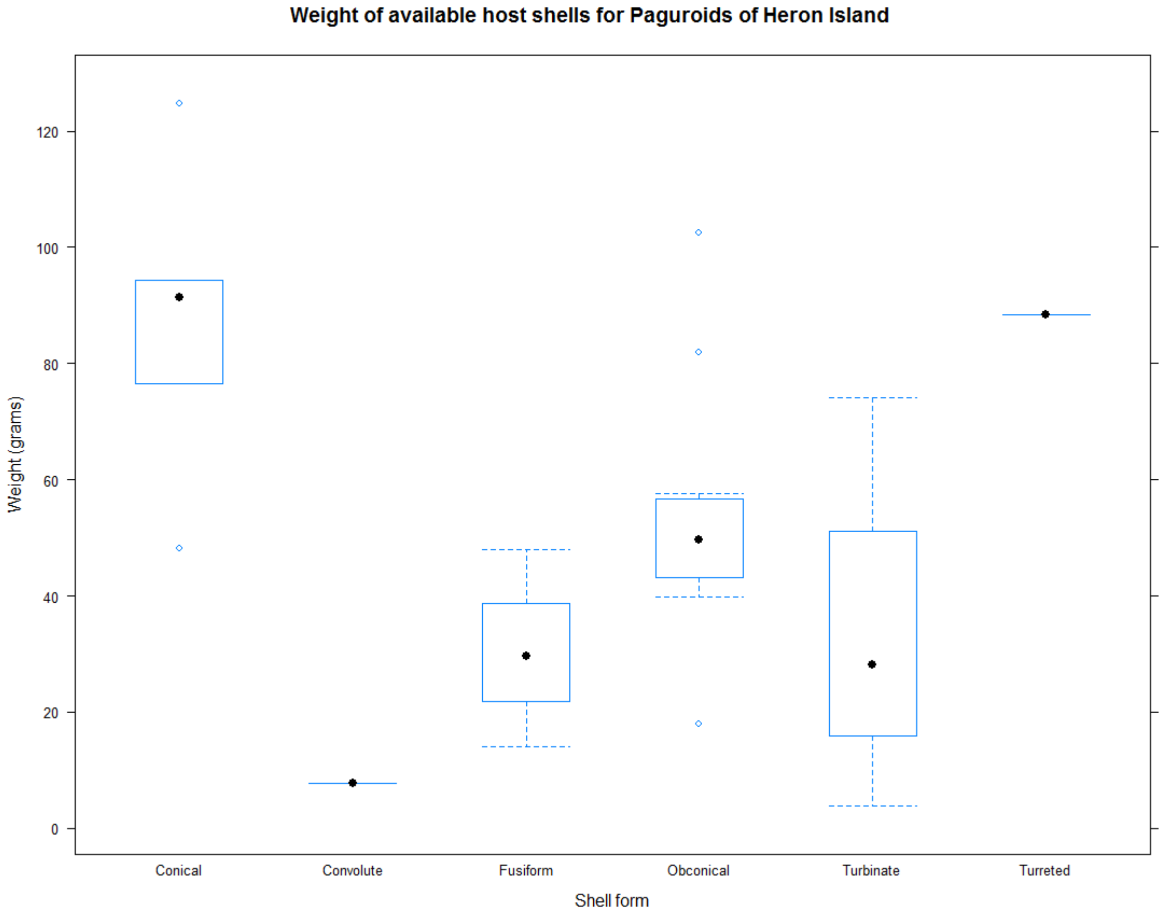

Figure 1. Gross weights (shell plus crab) of hermit crab shells collected from Heron Island, grouped by shell shape classes. The two largest shells, *Melo amphora* (1019 grams), occupied by *Dardanus megistos* and *Lambis lambis* (177 grams), occupied by *D. lagopodes*, have been removed for clarity.

C. gaimardii was recorded from smaller shells; a cowrie (*Cypraea sp.*), *Latirus polygonus*, a small *S. luhuans* and an unidentified turban snail. An individual was also recorded from the medium sized *Turbo argyrostomus*, of which *D. megistos* was also found.

Some shell forms recorded statistically faster emergence (Figure 2) and self-right (Figure 3) scores than others when considered across species. From pair-wise comparisons, crabs within obconical (*Conus, Strombus*) and fusiform (*Latirus polygonous*) shells emerged faster than those in conical shells (*Trochus*) ($p < 0.05$, Figure 2). At the host species level, crabs of *L. polygonous* and *S. luhuans*, but not *C. textile* emerged from shells faster than those of *Trochus* ($p < 0.05$, Figure 4). Further, there was moderate support ($p = 0.064$) for a difference between *C. textile* and *S. luhuans*. Similar pair-wise analysis for righting time only reported significance between conical and obconical shells ($p < 0.05$, Figure 3) and between *Trochus* and *S. luhuans* at the species level ($p < 0.01$, Figure 5).

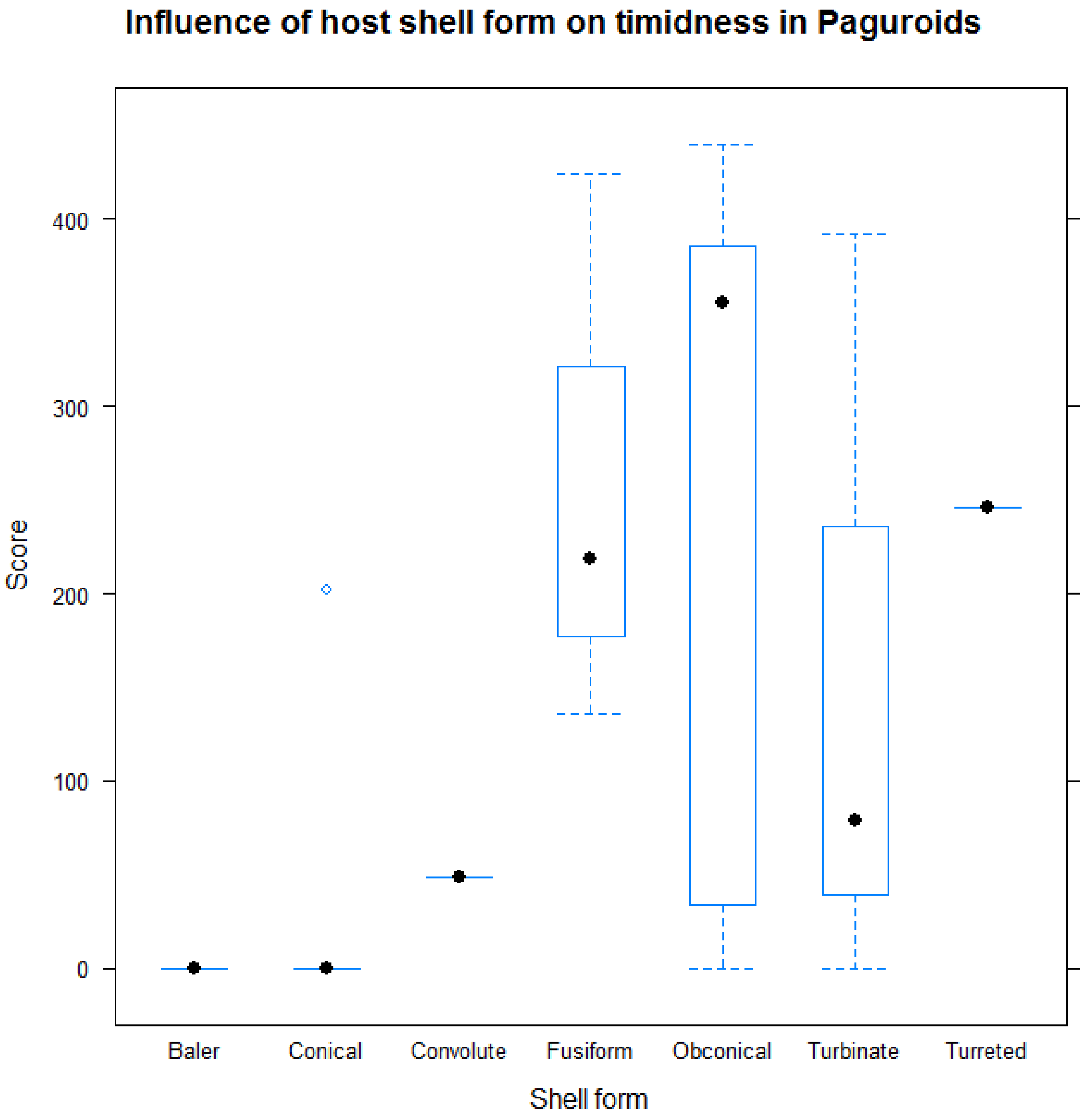

Figure 2. Influence on emergence behaviour of shell choice in hermit crabs of Heron Island. Shells are grouped according to shape classes. Scores range from 0 – 450, with higher values representing faster responses and a score of zero reflecting a trial where the crab did not emerge or emerged after a long period of inactivity.

The pattern between *Trochus* and *S. luhuans* was further supported from analyses within *D. dardanus*, for both emergence ($p < 0.05$) and righting ($p < 0.01$). Within group analysis was not considered for the other two diogenids due to lack of replication.

The individuals from the largest shells, *M. amhora* and *L. lambdis*, madeno attempt whatsoever to right themselves when left under laboratory conditions for several hours. These individuals were also left out of water for several hours but still made no attempt. The *D. lagopodes* of the *Trochus* shells were also very unresponsive. These crabs would emerge from their shell, unlike those of *M.amphora* and *L. lambdis,* but only after a considerable period time (Figure 3). Once emerged these crabs rarely made an effort to right in the laboratory, and only after several hours from commencement of the trial.
Once commited to righting itself, *D. megistos* was more efficient in doing so that *D. lagopodes* (p val = 0.06, Figure 6). There was, however, no apparent difference in emergence behaviour between the three species, as measured by emergence score.

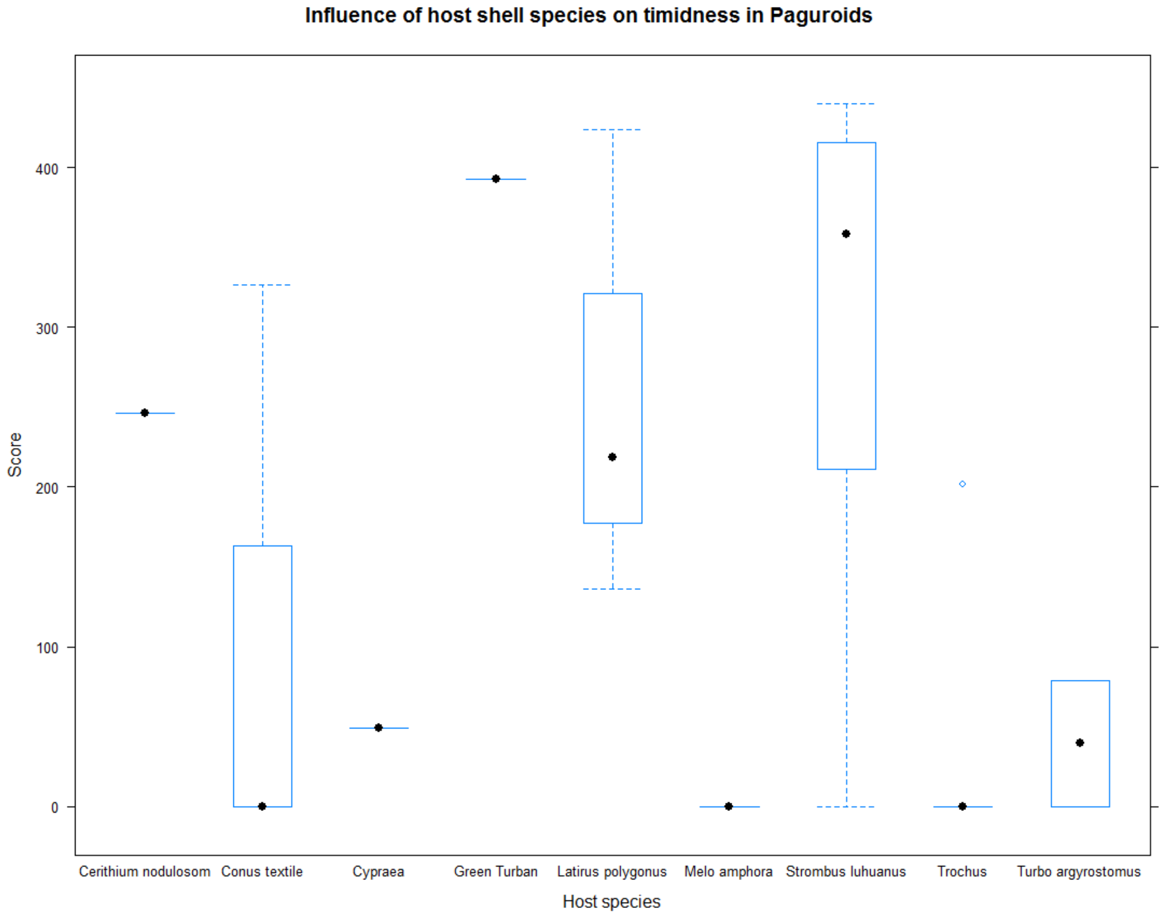

Figure 3. Influence on emergence behaviour of shell choice in hermit crabs. Scores range from 0 – 450, with higher values representing faster responses and a score of zero reflecting a trial where the crab did not emerge or emerged after a long period of inactivity.

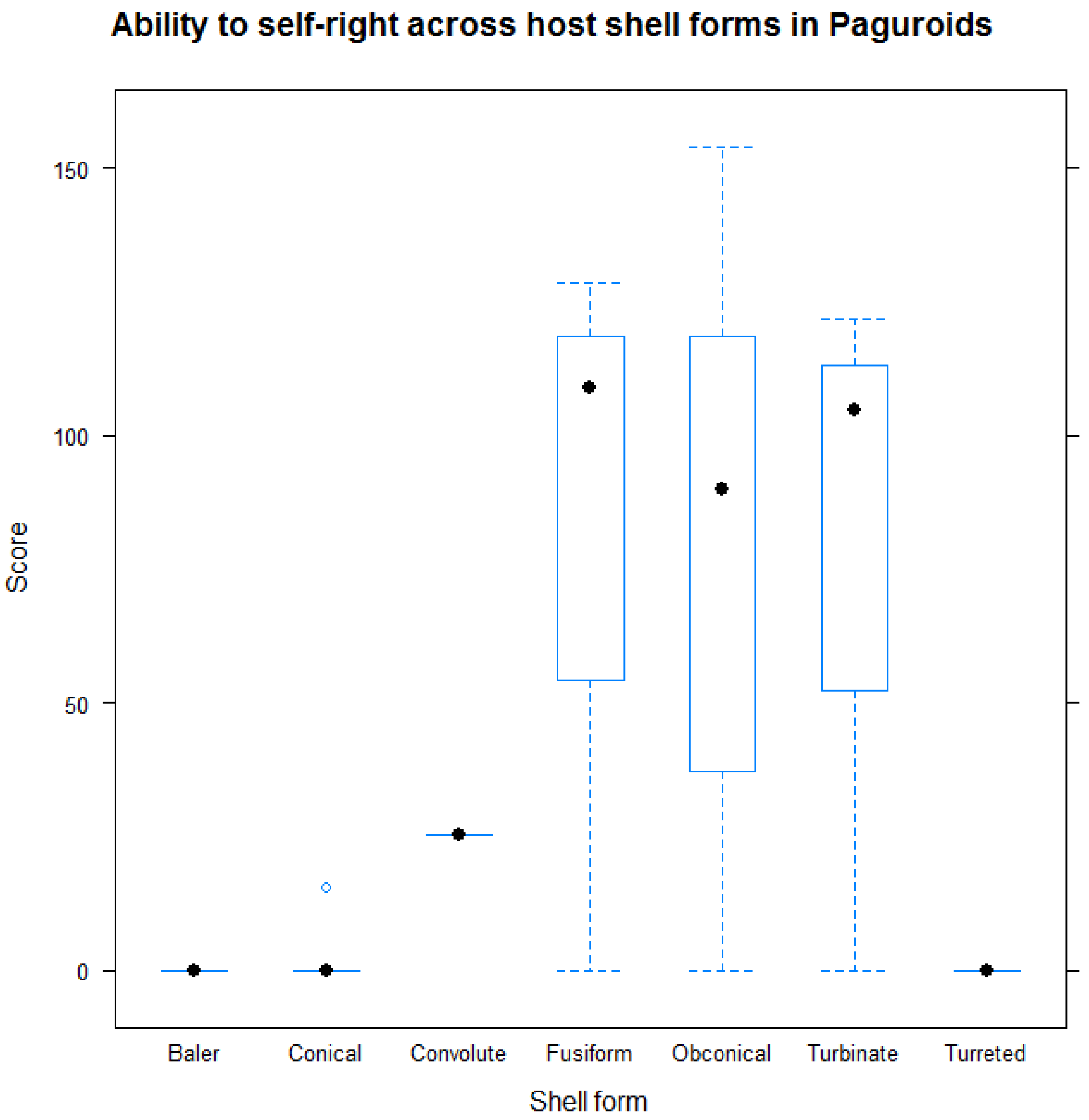

Figure 4. Consequence of shell choice in hermit crabs of Heron Island, measured as ability to self-right. Scores range from 0 – 172, with higher values representing greater ability to right and a score of zero reflecting a trial where no attempt was made for a substantial period of time. Shells grouped by shape classes.

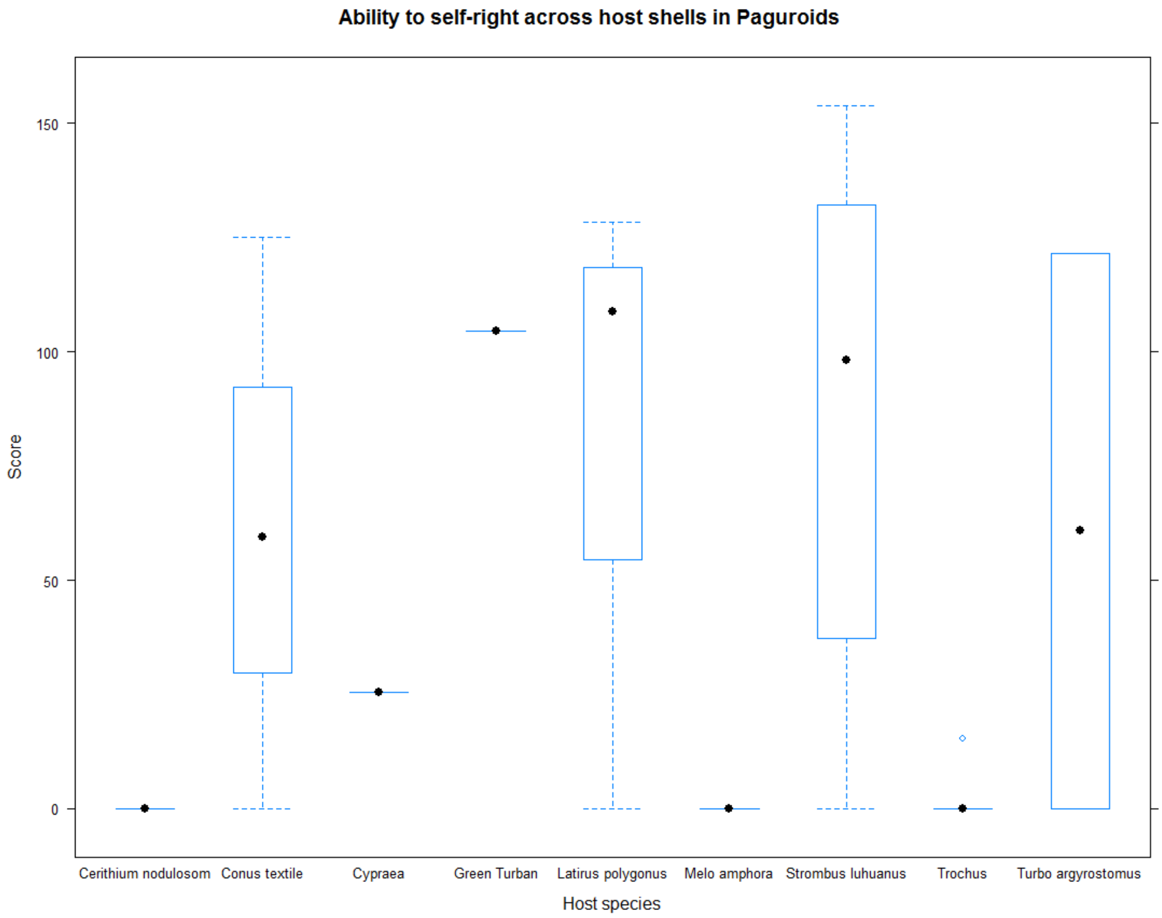

Figure 5. Consequence of shell choice in hermit crabs of Heron Island, measured as ability to self-right. Scores range from 0 – 172, with higher values representing greater ability to right and a score of zero reflecting a trial where no attempt was made for a substantial period of time.

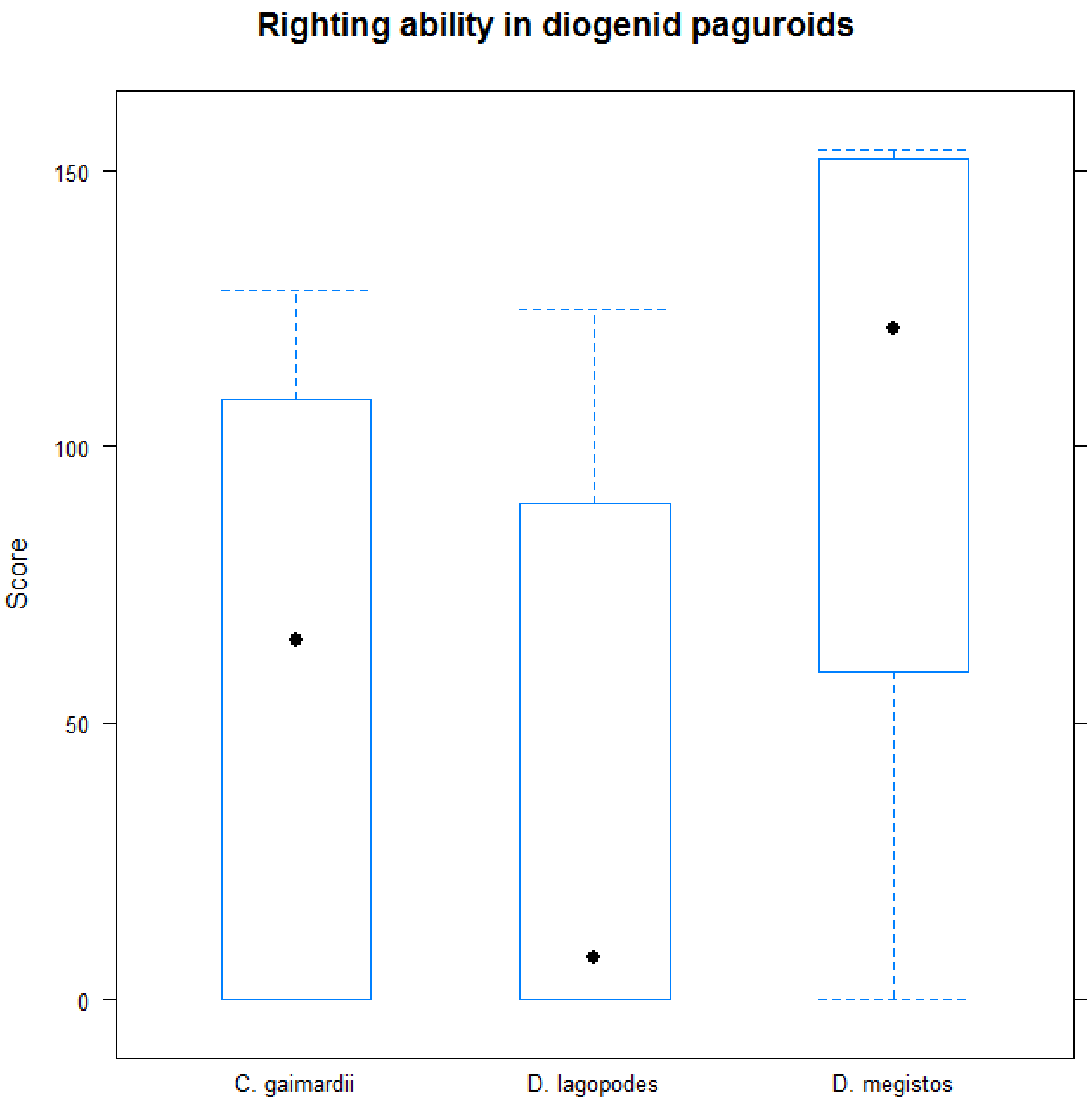

Figure 6. Ability to right when placed aperture upwards of three hermit crabs. Score ranges from 0 to 172, with a higher score reflecting less time taken to right from commencement of attempt. A score of zero represents a crab that did not begin to make an attempt after a considerable period.

Discussion

While evidence was found to suggest an influence of shell type, limitations of replication may hide further significant differences between the species and their hosts used. To address further questions it would have been of use to obtain measurements of crab body size in relation to its shell, particularly as relative weight has been previously demonstrated to influence shell choice (Reece 1962)

The relevancy of this study is undermined by a lack of confidence in the importance of the behaviours measured. How critical is it for a hermit crab to be able to right itself quickly? Certainly many of the individuals observed in this study appeared to be in no hurry, while others almost immediately re-emerged and began to haul themselves back over. Perhaps it is not true to generalise the need to right quickly. Provided a large and strong enough shell it is conceivable that a hermit crab could be better off aperture upwards than to expose its softer body parts in what is likely, for a heavier shell at least, an energetically costly task. Smaller individuals in weak, thin walled shells may be at much greater immediate risk.

Some shells, naturally, are more suitable for hermit crabs than others (Mantelattoand de Lucca Meireles 2004). The cowrie used by a *C. gaimarii* in this study for example would presumably not be an optimal shelter. Cowries have a very narrow aperture for their size, restricting the growth of the crab despite ample internal space. Further the aperture runs along the length of the ventral surface and so is difficult to shield with a cheliped, as in the classical defensive position (Forest *et al.* 2000). Finally, cowries are presumably more difficult to carry than typical gastropod shells, impeding movement.

Assessing the suitability of other shell types is more difficult, particularly when focusing on larger species of crab. Gastropod shells are well documented to be a limiting resource (Barnes 2001, Mantelattoand de Lucca Meireles 2004), and this of course is particularly so of larger crabs.Under this rationale there is perhaps little value in weighing the economics of shells such as *M. amphora* and *L. lambdis*. However it is interesting to note that the inhabitant of the conch in this study was still small enough to have fit inside a cone shell or stromb, the latter of which appear common in the area. This individual certainly wasn’t the largest *D. dardanus* and though no attempt was ever observed, the relative weight and awkward shape of the shell suggests that this individual would have little chance of righting itself. The large *D. megistos* on the other hand, though it too did not make an attempt, is considered to have easily been able to right itself, given its size relative to the shell and the large aperture and convenient shaping.

The *Trochus* shells can be thought of as representing a trade off. While they are heavy and cumbersome, greatly inhibiting the ability to self right, they also presumably afford very effective protection from predation. The shell is thick and the aperture normally rests almost flush with the ground, leaving little space for a predator attack. The hermit crab can also retract a considerable distance within the spiral and the aperture can easily be blocked by a cheliped. This arrangement should defeat most predators. A mantis shrimp will likely be deterred by the thickness of the shell, opting instead to search for an easier target and even an octopus would have difficulty extracting the crab from the narrow, tightly coiled aperture. The usage of the highly venomous cone shell by the hermit crabs raises an interesting possibility. Do hermit crabs seek out certain shells such as cones for the conceivable benefits of deterring potential predators? Or does shell usage simply reflect availability? If cone shells did afford any extra protection it would presumably be in the crabs interests to keep the shell clean, clearly advertising its lethalness with the distinct colouration and patterning. One of the cones found in this study was barely recognisable as such, though of course it cannot be known for how long the crab had been a resident. Conversely degraded shells such as these may be most desirable, offering the protection of crypsis through epibiotic communities (Briffa and Elwood 2005)

Irrespective of an ability to inspect and assess a shell, shell choice influences performance and most likely survival. Therefore investigating the determining the characters sought by hermit crabs in choosing a shell. Understanding performance costs and adaptation for optimisation is an interesting area of crustacean evolution and has revealed many further questions of the famously successful gastropod dependent lifestyle of hermit crabs.

Literature Cited

Barnes, D. K. A. 2001. *Ancient homes for hard-up hermit crabs*. Nature. 412: 785-786

Briffa, M. and Elwood, R. W. 2005. *Metabolic consequences of shell choice in* Pagurus bernhardus: *do hermit crabs prefer cryptic or portable shells*?

Forest, J., Laurent, M. de S., McLaughlin, P. A. and Lemaitre, R. 2000. *The marine fauna of New Zealand: Paguridea (Decapoda: Anomura) exclusive of the Lithodidae.* Wellington, New Zealand: National Institute of Water and Atmospheric Research

Mantelatto, F. L. and de Lucca Meireles, A. 2004. *The importance of shell occupation and shell availability in the hermit crab* Pagurus brevidactylus *(Stimpson 1859) (Paguridae) population from the southern Atlantic.* Bulletin of Marine Science. 75: 27-35

McLaughlin, P. A., Boyko, C. B., Crandall, K. A., Komai, T., Lemaitre, R., Osawa, M. and Rahayu, D. L. 2010. *Annotated checklist of anomuran decapod crustaceans of the world (exclusive of the Kiwaoidea and families Chirostylidae and Galatheidae of the Galatheoidea) – preamble and scope.* The Raffles Bulletin of Zoology. 23: 1-4

Reese, E. S. 1962. *Shell selection behaviour of hermit crabs*. Animal Behaviour. 10: 347-348

Wilson, B. 2002. *A handbook to Australian seashells on seashores east to west and north to south*. Sydney, Australia: Reed New Holland