Shell Selection and Behavioral Responses to Predators in the Intertidal Hermit Crabs of Puget Sound

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Abstract:

Intertidal hermit crabs of Puget Sound include *Pagurus hirsutiusculus*, *P. granosimanus*, and *P. beringanus*. Both *P. granosimanus* and *P. beringanus* individuals were found in shells about four times their body weight while *P. hirsutiusculus* were typically in shells slightly lighter than body weight; except for gravid females that carried shells nearly twice their body weight. Unlike *P. granosimanus* and *P. beringanus*, which always retreat into their shells when picked up, 73% of *P. hirsutiusculus* (n=126) abandon their shells. Gravid female *P. hirsutiusculus* were less likely to display this behavior - only about 23% abandoned their shells. *P. hirsutiusculus* is an especially active hermit crab; after being startled by a controlled thump on its holding tank a crab would recover normal behavior in about 6 sec.; *P. granosimanus* took twice as long. When placed in water that had previously contained rapidly moving, visual and chemosensitive predators (either *Cancer productus* or *C. magister*), *P. hirsutiusculus* displayed the same or a slower recovery from the startle stimulus while the behavior of *P. granosimanus* remained unchanged and relatively slow. In contrast, hermit crabs exposed to water that had contained the slow moving, chemosensitive predatory starfish *Pycnopodia helianthoides* either retained their high recovery rate (*P. hirsutiusculus*) or increased it (*P. granosimanus*). These findings suggest that *P. hirsutiusculus* is a “shell minimalist” selecting small, relatively lighter shells that it readily abandons, relying on quick escape behavior in the presence of slow moving predators. These behaviors are modified in gravid females or in the presence of rapidly moving visual predators.
Hermit crabs are unique among crustaceans in that they have a soft abdomen that is unprotected by a hard exoskeleton (Headstrom, 1985). The abdomen is instead protected by a foreign object that the crab carries or wears – most commonly a snail’s shell. As the crab grows, its abdomen becomes shaped by the shells it occupies and the abdomen spirals in order to better fit the whorl of the shell (Headstrom, 1985). Most hermit crabs can even withdraw completely into this borrowed shell and close the opening of the shell with their larger right cheliped (Headstrom, 1985). A hermit crab is extremely vulnerable without this protection and usually it hangs tightly onto the interior of the shell with small hooks at the end of its abdomen (Headstrom, 1985). These hooks are actually the last pair of legs normally found in crabs that have been modified in order to secure the crab into its shell (Headstrom, 1985). These hooks are so strong that hermit crabs can be torn in half if pulled by their cheliped and legs because the strength of the hook’s grip on the shell is stronger than the connective tissue of the cheliped and legs to the body. Their abdominal hooks can so tightly attach to the interior of the shell that one cannot simply pull out a crab without causing it major bodily harm (Street, 1966).

Three intertidal species found in San Juan Island are *Pagurus granosimanus*, *Pagurus beringanus*, and *Pagurus hirsutiusculus* (Hart, 1982). Both *P. granosimanus* and *P. beringanus* have been observed as having typical hermit crab behavior and withdraw into their shell when picked up (Headstrom, 1985). However, *P. hirsutiusculus* displays a unique behavior in that when this crab is picked up by its shell it will often abandon the shell and flee (Ricketts et al., 1985). This behavior can be considered
bizarre amongst hermit crabs not only because it leaves the abdomen of *P. hirsutiusculus* vulnerable to damage, but also because shell selection is typically a very selective and time consuming process for hermit crabs (Street, 1966).

Given this variation in behavior, is there a difference in shell selection amongst these three species of crabs? The reported shell abandonment (Ricketts et al., 1985) of *P. hirsutiusculus* could suggest that it is less picky about its shell compared to other hermit crab species or that it is incapable of finding a better fitting shell. If this is true, then the relationship of the shells of *P. hirsutiusculus* to its body size should be different than the other two species. If *P. hirsutiusculus* has a different shell selection strategy, that may suggest that it interacts with predators in a different way that *P. granosimanus* and *P. beringanus*. *P. hirsutiusculus* seems more nimble and less dependent on its shell for protection, if this is the case then in the presence of predators it should react differently than the other two species. Utilizing a light shell may mean depending on agility or speed to escape predators and *P. hirsutiusculus* may have a faster response to stimulus than *P. granosimanus* or *P. beringanus* in the presence of predators.

Materials and Methods

Hermit crabs of all three species were collected by hand from three locations on San Juan Island; Garrison Bay, Cattle Point, and False Bay and brought back to the Friday Harbor Laboratories. In the lab, the hermit crabs were kept in separate tanks or containers in a sea table with flow-through circulation according to their origin. The
crabs were given *Ulva lactuca* and some rocks in their containers in order to provide cover and food.

*Measurements and Shell Releasing Trials:*

In order to weigh the shell mass and crab mass separately the crabs were removed from the shell in three different ways. For *P. hirsutiusculus*, crabs were picked up and suspended by their shell and the crab often released its hold on the shell and fell out. Another useful tactic in getting *P. hirsutiusculus* crabs separated from their shells was to sharply tap the back of the shell of a suspended crab. This would often cause the crab to release its grip on the shell and fall out. *P. granosimanus*, *P. beringanus*, and some *P. hirsutiusculus*, most notably a large percentage of gravid *P. hirsutiusculus* females, required a different method of removal since they did not displaying shell release behavior. These crabs were first weighed with their shell on and then pliers were used to chip away the back of the shell and a probe was used to gently prod the soft abdomen of the crab until it finally released its hold on the shell. The naked hermit crab was then weighed and the shell mass was found by finding the difference in mass from the crab’s weight and the combined weight of the shell and crab. Separate shells and crabs were blotted dry, however, when crabs and shells were weighed together it is likely that a small amount of water deep within the whorls of the shell added to the measured weight of the crab and shell combination. Each crab’s major cheliped length and width, and carapace length were measured with calipers. The aperture of each shell was measured at its widest point. A record of which hermit crabs were carrying eggs was kept.
Videos were taken of each crab being picked up by its shell to record its response and the timing of its behaviors. Handling crabs excessively before testing for shell release tended to increase the variance in their behaviors (e.g. *P. hirsutiusculus* that were recently handled seemed more likely to retain their shell), so to minimize this variation, hermit crabs were housed undisturbed for at least 24 hours in a tank prior to measurement and during the test were picked up from that tank by hand which proved a firmer grip and a more consistent process than using forceps.

*Predator Trials:*

In order to assess a difference in behavioral responses to predators between *P. granosimanus* and *P. hirsutiusculus* predator trials were set up. In general, our procedure was based on that of (Rosen et.al, 2009). Three different predator species were used in these trials; two species of crabs, *Cancer magister, Cancer productus*, that use both visual and chemosensory information in finding prey (Ricketts, et al., 1985), and the starfish *Pycnopodia helianthoides* that relies primarily on chemosensory information for hunting (Yagoda, 2004). Each predator was placed in a separate plastic bucket containing six liters of water without flow for two hours. This ‘predator water’ served as the experimental treatment in a given set of experiments. Seawater drawn from the FHL seawater system was used as the comparison. In each experiment, we used 35 newly collected hermit crabs of each species (*P. granosimanus* and *P. hirsutiusculus*). One liter of seawater or predator-flavored water was put into a white plastic container measuring 11 cm by 11 cm by 11 cm. A frame was placed next to the container and a 29 gram weight was used as a pendulum, suspended from the top of the frame by 30 cm of fishing line. I provided a consistent stimulus for startling the crabs by lifting the pendulum on
the string so that it was 33 cm above the table and perpendicular to the top of the PVC frame and then letting it drop so that it hit the side of the container once.

At the beginning of a trial, a crab was placed aperture side up in the test container. If the crab showed no movement within ten seconds it was not used and a new crab was chosen. Each hermit crab was given 100 seconds to flip over and explore the container. Once the 100 seconds were up, the pendulum was picked up and dropped to hit the container. From videos taken of each test, I measured the lag time between the startle stimulus and when the crabs resumed their normal posture or behavior. Behavior was considered normal when the crabs resumed normal posture with legs extended beyond the margin of the shell rather than being withdrawn.

Each crab was exposed to seawater and the predator water of only one species of predator (these two trials occurred not less than 15xx minutes apart). Half of the crabs were tested in seawater first, and predator water second, the other half were treated in the reverse order. An experiment proceeded by alternating five individuals of one crab species (tested separately) and then five individuals of the other species. The water in the test container was refreshed after every fifth crab and switched from seawater to predator water (or visa versa) every tenth crab. Throughout the experiment, the seawater was 12 C to 13 C in temperature while predator water was 14 C in temperature.
Results

In all three species there was a significant linear relationship between shell mass and body mass \((P. \text{granosimanus}, y = 4.98x + 0.33, n= 55, \text{Spearman rho} = 0.84, p<0.0001; P. \text{beringanus}, y= 4.13x + 0.19, n = 13, \text{Spearman rho} = 0.91, p<0.001; P. \text{hirsutiusculus}, y=0.90x -0.04, n=120, \text{Spearman rho} = 0.86, p<0.003)\) (Figure 1). In all three relationships, the intercept of the regression lines were not different than zero \((t=7.14, n=55, p=0.48; t= 0.19, n=13, p=0.26; t = -1.56, n=120, p= 0.13\) respectively). The slopes of \(P. \text{granosimanus and P. beringanus}\) were not significantly different from each other \((\text{Wilcoxon Rank Sum, } X^2 = 0.001, \text{d.f.} = 1, p=0.99)\). Animals from each of these species typically carry a shell that is more than four times its body weight. This differs from \(P. \text{hirsutiusculus}\) \((\text{P.g. vs. P.h. Wilcoxon Rank Sum, } X^2 = 94.84, \text{d.f.} = 1, p<0.001, \text{P.b. vs. Ph Wilcoxon Rank Sum, } X^2 = 30.26, \text{d.f.} = 1, p<0.001)\) which is typically carrying a shell that is slightly less than its body mass (Figure 1).

The berried, or egg carrying, females of \(P. \text{granosimanus}\) did not have a regression line significantly different than the non-berried individuals of \(P. \text{granosimanus}\). This is in contrast to the pattern in \(P. \text{hirsutiusculus}\) where the berried females have shells that weighed about twice as much as those individuals without eggs \((\text{slopes of 2.09 and 0.902 respectively})\) (Figure 2). This suggests that berried female \(P. \text{hirsutiusculus}\) change their shell selection behavior compared to individuals without eggs.
Crabs were picked up by their shell in order to test for shell release behavior. 68 *P. granosimanus* and 12 *P. beringanus* were tested for shell release behavior. None of the crabs from these two species released their shells. Of 126 *P. hirsutiusculus* crabs that were tested, 73% released their shells when picked up. Of the 33 *P. hirsutiusculus* individuals that did not release their shell, ten were berried females. Overall, only three out of thirteen berried female *P. hirsutiusculus* released their shells.

The predator trials conducted with *P. granosimanus* and *P. hirsutiusculus* showed significant differences between the two species in their behavior in seawater and predator water. In the seawater control for all three predator trials and in the predator water for each predator, *P. hirsutiusculus* was faster to begin movement after being startled than *P. granosimanus*. For *Cancer magister* water, *P. hirsutiusculus* was significantly slower in its reaction to being startled in the predator water than in seawater. However, *P. granosimanus* reactions in seawater and predator water were not significantly different.

For *Cancer productus* water, neither *P. hirsutiusculus* nor *P. granosimanus* had significantly different reactions between seawater and the predator water. In the *Pycnopodia helianthoides* water, *P. granosimanus* had a significantly faster reaction time than in the control seawater. *P. hirsutiusculus*, however, had no significant difference between the control seawater and the predator water in reaction times.

Discussion

**The advantages and disadvantages of small shells**

The behavior of the intertidal hermit crabs *P. hirsutiusculus* differs greatly compared to of the other two intertidal hermit crab species (*P. granosimanus* and *P.*
beringanus) of Puget Sound. Both *P. granosimanus* and *P. beringanus* are found in shells approximately four times their body weight and they can withdraw completely into these protective shells. In contrast, *P. hirsutiusculus* carries shells that were either of the same weight as the crab or slightly lighter and these lighter shells require less energy to carry and allow *P. hirsutiusculus* to move quicker. This suggests that *P. hirsutiusculus* depends on agility and speed to escape predators. When *P. hirsutiusculus* individuals are grabbed by the shell, the shell-release behavior allows them to escape rapidly, however, it is at the expense of having their abdomen exposed for an unknown amount of time until they find a new shell. These relatively small shells do not allow *P. hirsutiusculus* to withdraw completely into the shell and the crabs could be easily ripped out by a predator. Thus, shell release rather than shell withdrawal may be beneficial for *P. hirsutiusculus*.

The behavior of the berried females choosing shells twice their weight and not displaying the shell release behavior as commonly as non-berried individuals could be an indication that these crabs are not willing to expose their abdomen and eggs. In contrast, berried *P. granosimanus* and non-berried *P. granosimanus* do not behave differently in regards to shell size or shell retention behavior suggesting that their larger shells can accommodate both a crab and her eggs.

**Response to predators**

The quick reaction to being startled by *P. hirsutiusculus* in comparison to *P. granosimanus* in both seawater and predator water is consistent with my hypothesis that *P. hirsutiusculus* uses speed and a light shell to escape from predators rather than withdrawing into a heavy shell. *P. granosimanus* had no significant difference between
seawater and *Cancer magister* predator water, while *P. hirsutiusculus* responded approximately twice as slowly. This may be a way to avoid attracting the attention of a nearby visual predator. Neither *P. granosimanus* nor *P. hirsutiusculus* changed their behavior in the presence of the scent of *Cancer productus*. This could suggest that they are unfamiliar with this predator (unlikely because it was found in habitats in which they were collected), that the scent stimulus was not strong enough, or that the two *Cancer* species have different predation responses to hermit crabs. In the presence of water scented with the starfish, *Pycnopodia helianthoides*, both species of hermit crabs had rapid recovery from the startle stimulus suggesting that there is an advantage to moving away from a *Pycnopodia* as quickly as possible.

The behaviors of *P. granosimanus* and *P. beringanus* are unsurprisingly similar to each other since both are a species of hermit crab living in the same environment. The behavior of *P. hirsutiusculus* is distinct in that it has become a shell-minimalist. This species chooses small light shells and scampers away quickly from most threats rather than withdrawing into a shell for protection, the exception being when the movement itself might draw the attention of a predator.
Figure 1. The relationship of shell mass versus crab mass for *P. granosimanus*, *P. beringanus*, and *P. hirsutiusculus*. All three lines have an origin not different than zero. The slopes of the regression lines of *P. granosimanus* and *P. beringanus* were not significantly different from each other (4.99, n=68 and 4.13, n=13 respectively) and both were significantly different than *P. hirsutiusculus* (slope of 0.90, n =120).
Figure 2. The relationship of shell mass versus crab mass in berried and non-berried individuals of *P. granosimanus* and *P. hirsutiusculus*. *P. granosimanus* individuals with eggs and those without did not have a significant difference in their regression lines. *P. hirsutiusculus* individuals with eggs had regression line slopes of 2.09 while those without eggs had a regression line of 0.90 indicating that the berried individuals of *P. hirsutiusculus* select larger shells when carrying eggs while *P. granosimanus* females do not. All regression lines have origins not different than zero.
Figure 3. Shell release behavior for three species of intertidal hermit crabs. No individuals of *P. granosimanus* (n=68) or *P. beringanus* (n=12) released their shells when picked-up. In contrast, 73% of *P. hirsutiusculus* (n=126) crabs release their shells. Of the *P. hirsutiusculus* that did not release their shells, one third were berried females (e.g. only 3 of 13 berried female *P. hirsutiusculus* released their shells).
Literature Cited


