Hermit crab houses: an analysis of shell selection patterns in three Monterey Bay *Pagurus* Species

Research Proposal

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Abstract

Hermit crabs are widespread detritivores in intertidal ecosystems. They are crustaceans that spend their lives inside the empty shells of deceased snails, using the shells for growth, reproduction, and protection. As a result, they are entirely dependent on snail populations, and any shift in these snail populations due to climate change or other anthropogenic factors could significantly impact hermit crab populations. Prior research suggests that different species have preferences for different types of shells. This study would investigate the shell preferences of *Pagurus samuelis*, *Pagurus hirsutiusculus*, and *Pagurus granosimanus*, the three most common hermit crabs in Monterey Bay rocky intertidal zones, and determine whether or not competition impacts their shell selection. Preliminary experiments involved removing individuals from their shells, placing them in a tank with an array of different shells, and recording which shells they ultimately chose to inhabit. Species were tested in isolation, so that interspecific competition did not affect shell selection. My results demonstrated that both *P. samuelis* and *P. hirsutiusculus* have a significant preference for *Tegula funebralis* shells, though the preference was much more pronounced for *P. samuelis*. *P. granosimanus* exhibited no significant preferences. Should I receive funding, future work will expand the sample size to verify the trends from the initial experiment. Future experiments will also involve multispecies trials to assess how competition affect shell selection. Finally, ecosystem-level experiments would be useful to determine how a change in snail populations might impact each species of hermit crab.

Introduction

Hermit crabs are decapod crustaceans that live in intertidal environments throughout the globe. They are detritivores, feeding on a wide variety of decaying plant and animal material

(Hazlett, 1981), and, in California they are the dominant scavengers in rocky intertidal zones (Greggor & Laidre, 2016). Thus, they play a critical role in decomposition and nutrient cycling in intertidal ecosystems. Hermit crabs have adapted to occupy empty snail shells. Evolution has made them entirely dependent on these shells for survival (Hazlett, 1981). Lacking a calcified abdominal exoskeleton, they rely on shells for shelter, growth, reproduction, and protection from predation, desiccation, and physical abrasion (Hazlett, 1981; Greggor & Laidre, 2016). Metamorphosis produces individuals with asymmetric, coiling abdomens perfectly suited to fit inside snail shells (Laidre, 2011).

Hermit crabs cannot remove snails from their shells; they only inhabit already empty shells and are known to switch shells frequently (Laidre, 2011). As they grow, larger shells become more desirable. Studies have shown that most species are opportunistic when selecting shells. If they encounter a more desirable shell, they will abandon their previous shell in favor of the new one (Hazlett, 1981). In rocky intertidal zones with hermit crabs, empty shells are scarce, and on average, hermit crabs occupy shells smaller than their preferred size because competition forces them to accept these less desirable shells (Hazlett, 1981; Laidre, 2011).

Understanding the nuanced shell preferences of hermit crabs is important because the distributions of many species and the dynamics of communities are changing in response to climate change (Travis et al., 2013). Shifting ranges in hermit crab and snail species could change the availability of certain shell types to hermit crabs and have significant implications for the success of hermit crabs in various regions. Warming and other anthropogenic impacts also have the potential to generate trophic cascades that impact the abundance of certain snail species, and therefore, the availability of shells to hermit crabs (Paine, 1969; Gravem & Morgan, 2017).

If the availability of preferred shells decreases, it is important to know whether hermit crabs will have a suitable alternative or if they will decline as well. Likewise, if a different snail species increases in abundance and leaves more shells, we should understand whether hermit crab species will benefit from this change. Any changes in the success of hermit crabs resulting from changes in snail populations could have significant consequences for nutrient cycling in intertidal ecosystems.

Previous studies of shell selection suggest that all species of hermit crabs prefer shells that have not been subjected to significant wear (Bulinski, 2007) and that different species of hermit crabs prefer different shell types (Hahn, 1998; Absher et al., 2001; Ko & McLaughlin, 2008). As noted above, there is also evidence that interspecific competition affects shell choice. For example, *Pagurus granosimanus* inhabit smaller shells when in the presence of the more aggressive *Pagurus samuelis* (Hazlett, 1981). Past studies have shown shell preference for *Tegula* in *P. samuelis* and *P. granosimanus* (Hahn, 1998; Absher et al., 2001; Ko & McLaughlin, 2008). One study found that *P. samuelis* is more likely to be found in *Tegula funebralis* shells, while *P. granosimanus* is more likely to be found in *Tegula brunnea* shells. There is less information on the shell preference of *Pagurus hirsutiusculus.* Evidence indicates that it prefers more elongated shells, such as *Littorina* and *Nucella*, as opposed to the more rounded *Tegula* shells (Worcester & Gaines, 1997; Straughan & Gosselin, 2014). Additionally, information on the degree to which interspecific competition affects selection of shell species is limited. For example, it is unclear why *P. granosimanus* are more likely to be found in *Tegula brunnea* shells than is *P. samuelis* (Hahn, 1998). Perhaps *P. granosimanus* actually prefers *T. brunnea* shells, or perhaps competition for *T. funebralis* with the dominant *P. samuelis* forces them to take less desirable *brunnea* shells. Alternatively, there may simply be more *T. funebralis* shells in *P. samuelis*-favored areas and more *T. brunnea* shells present in *P. granosimanus* dominated areas. Finally, few studies have removed the preferred shell type to assess whether each species has another alternative, which could be important in determining how hermit crabs respond to changes in snail populations.

This study will assess the priorities of the three common *Pagurus* species of Monterey Bay (*P. samuelis*, *P. granosimanus*, and *P. hirsutiusculus*) in selecting shells. Preliminary laboratory experiments involve collecting hermit crabs of all three species and placing individuals in tanks with shells of different sizes and snail species and to observe which shells the crabs choose to inhabit.

Methods

The species most commonly found in the intertidal zone in Monterey Bay are *Pagurus samuelis, Pagurus granosimanus*, and *Pagurus hirsutiusculus*. *Pagurus samuelis* has a red head and antennae with blue patches on the tips of its legs, and its carapace is olive green. This species is typically found in mid to high intertidal protected zones (Absher et al., 2001). *Pagurus granosimanus* is dark olive green, with wart-like granules on its legs and claws. It is most often found in lower intertidal and subtidal areas (Ko & McLaughlin, 2008). The third species found on the rocky shores of Monterey is *Pagurus hirsutiusculus*. It is characterized by white bands on its legs and antennae as well as the large amount of hair covering its body. This species is less common than the other two species (Worcester & Gaines, 1997; Straughan & Gosselin, 2014).

I began my work by learning to identify the different species of hermit crabs and the species of snail shells that they inhabit. Observations from the intertidal zone confirmed trends in the literature suggesting that *P. samuelis* and *P. Granosimanus* typically occupy *Tegula* shells, while *P. hirsutiusculus* inhabit other types of shells such as *Nucella* and *Littorina*.

Next, I conducted laboratory trials. I collected an assortment of shells and placed them haphazardly throughout a 29 x 18 cm tank filled with seawater at approximately 15℃. Each trial involved three hermit crabs of the same species and lasted for two hours. I began each trial by removing the hermit crabs from their original shells. To accomplish this, I used pliers to clip off the tips of each shell as far as was necessary to expose each hermit crab's rear end. Occasionally, I clipped the crab itself, in which case I found another crab to replace the damaged one. I then held the hermit crabs over a tank filled with seawater and poked their rear ends until they moved forward out of their shells and fell into the tank. I recorded the original shell as well as the first shell that each hermit crab chose to inhabit. Finally, I recorded the shell that each individual inhabited after two hours.

I tested 45 individuals in total over 15 trials--5 trials and 15 individuals for each species. Individuals of the same species were tested together to eliminate any impacts related to interspecific competition. Before each trial, I ensured that the tank contained at least five different shells of each common shell type from the intertidal--7 each of *Tegula Funebralis Tegula Brunnea*, and *Nucella,* and five each of *Ceratostoma*, *Olivina*, and *Littorina*. It was difficult to find empty specimens of the latter three shell types and they were rarely chosen by the hermit crabs, hence the lower number in the tank. I also ensured that those five shells were roughly similar in size to the shells from which the hermit crabs were extracted. Exact shell sizes of each shell inhabited by the crabs were not measured; however, several shells of each type were measured to get an idea of the size. The *Tegula* shells were generally 1.3-1.5 cm x 1.3-1.5

cm, while the other more elongated specimens were generally 2.5-3 cm x 0.9-1.3 cm (length x maximum width at opening). In future trials, I plan to record shell size to include it as a predictor. New shells were added to the tank before each trial as necessary to meet these criteria. This minimized the impact of intraspecific competition on shell preference and eliminated the variation in abundance of different shell types that is found in the intertidal, allowing me to observe what the most preferred shells were, rather than the simply the most commonly inhabited shells. The two hour time limit was adopted because during the first three trials (one with each species), hermit crabs stopped switching shells after the first hour. Thus, two hours was a conservative time interval, ensuring that the shell recorded at the end of the trial was likely their most preferred shell in the tank.

Data Analysis

After the data were collected, I organized it by analyzing proportions. For each hermit crab species, I calculated the proportion of individuals that were found in each shell type originally (labelled Original_Shell) and plotted these proportions using ggplot 2. The same was done for the shells that individuals of each species first occupied during the trials (labelled First_Shell) and for the shells that they were found inhabiting at the end of the trials (labelled Final_Shell). A chi-squared test was run on Final_Shell proportions for each species to test whether any of the species exhibited a significant preference toward certain shell types.

Preliminary Results and Discussion

The data suggest that *Pagurus samuelis* have a significant preference for *Tegula funebralis* ($p = 1.75 \times 10^{-8}$). Initially, nearly all *Pagurus samuelis* were found in *Tegula funebralis* shells (Fig 1). After removal from original shells, only around 50% of the *P. samuelis* initially went into the *Tegula funebralis* shells (Fig 2). At the end of the trials, an overwhelming majority of *P. samuelis* were found to inhabit *T. funebralis* (Fig 3), indicating that the hermit crabs switched to *T. funebralis* from less desirable shells over the course of the trials. The data also suggest that *P. hirsutiusculus* exhibited a tendency to choose certain shell types over others, though this preference is much weaker than for *P. samuelis* (p = 0.04). *Pagurus hirsutiusculus* seems to exhibit a slight preference for *T. funebralis* and avoids *Olivella* (Fig 3), although the proportion of individuals found in *T. funebralis* decreased from what was observed prior to the trials (Fig 1). *Pagurus granosimanus* exhibited no clear preferences for shell type (p = 0.29). A majority were originally found in *T. funebralis* shells (Fig 1); however, the amount of *T. funebralis* occupied decreased considerably by the end of the trials (Fig 3), indicating that the initial prevalence of *T. funebralis* may be simply due to their high abundance in the intertidal zone. Interestingly, *P. granosimanus* were the only species ever found in *Olivella*.

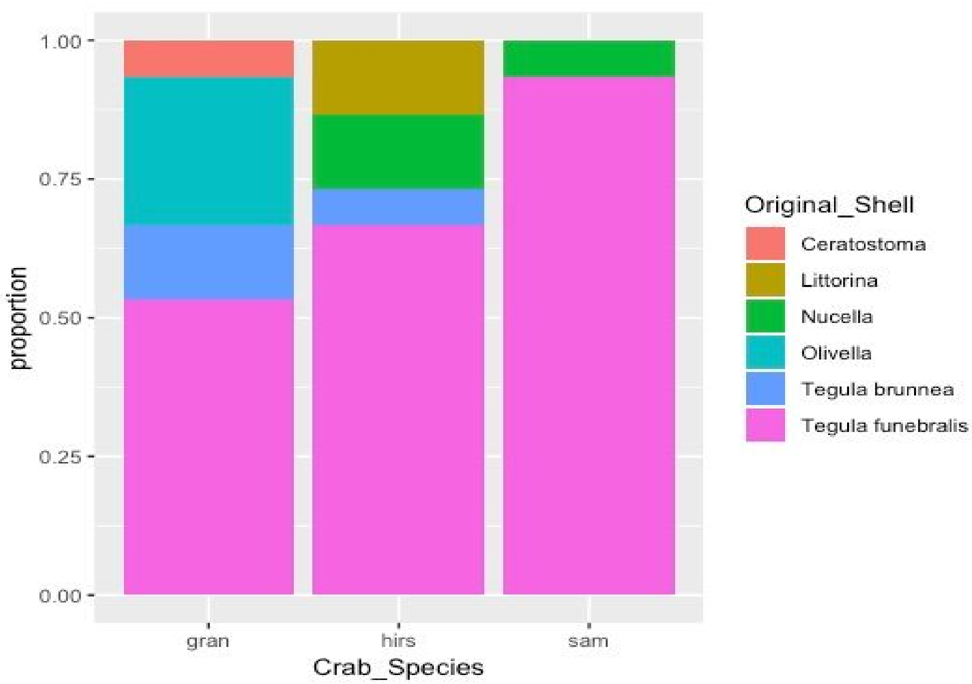

Fig 1: Proportion of the total number of individuals of each hermit crab species inhabiting different shell types prior to the trials.

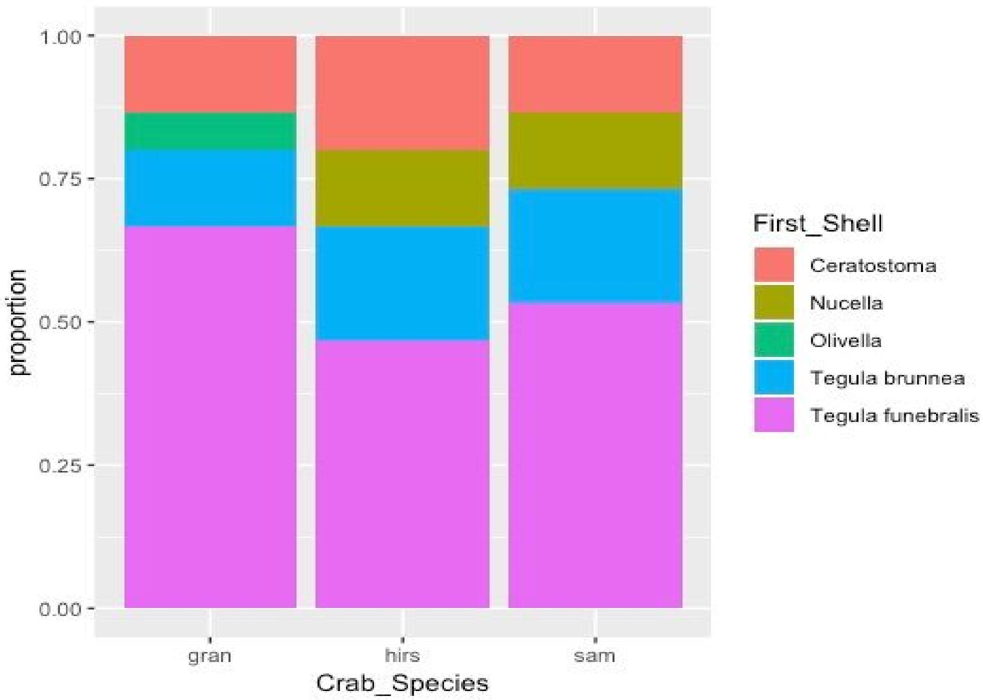

Fig 2: Proportion of the total number of individuals of each hermit crab species that chose different shell types immediately following removal from original shells.

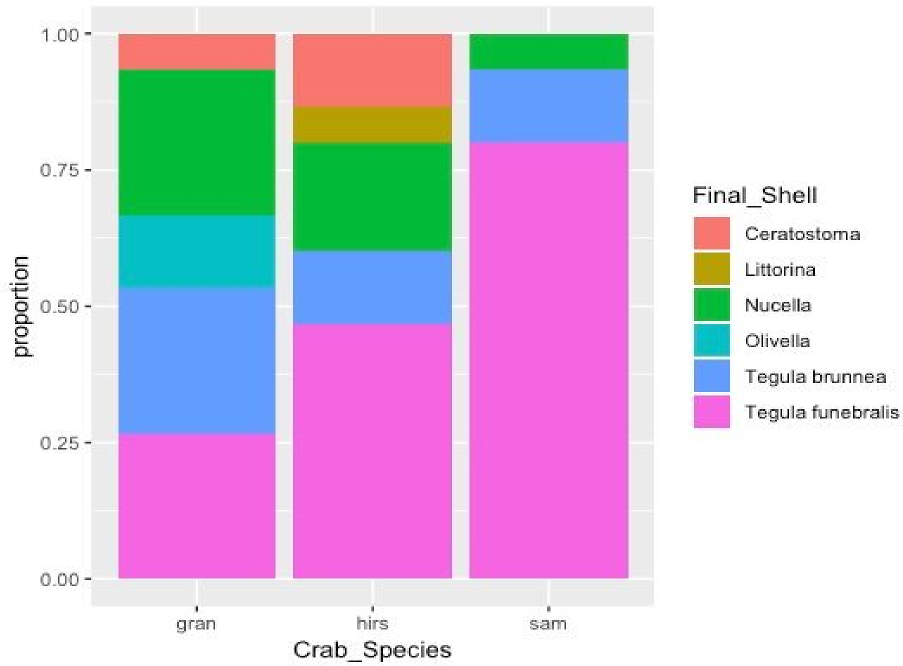

Fig 3: Proportion of the total number of individuals of each hermit crab species inhabiting different shell types at the end of a two hour trial.

The preliminary results confirm that *Pagurus samuelis* prefer *Tegula funebralis*. Nearly all of the *P. samuelis* were originally found in *T. funebralis* shells. After removal, they generally went into the first suitable shell that they found, but the majority shifted to *T. funebralis* shells by the end of the trial periods, indicating that they were actively choosing *T. funebralis* shells. No clear trends emerged in the preferences of *P. granosimanus*. Thus, *P. granosimanus*' tendency to be found in *Tegula* shells may be simply due to the overwhelming abundance of these shells in the intertidal. It is also possible that *P. hirsutiusculus* outcompetes *P. granosimanus* for other shell types. My results for *P. hirsutiusculus* are not consistent with the literature. Most *P. hirsutiusculus* were initially found in *Tegula* shells, perhaps due to their abundance. If they preferred *Nucella* or *Littorina* shells, I would have expected to see a decrease in the amount of *Tegula* occupied by the end of the trials; however, this did not occur to a significant degree.

Although there was a small decrease in *Tegula* occupation, *P. hirsutiusculus* still showed a significant preference for *Tegula* shells, with a clear majority of individuals inhabiting these shells at the end of the trials. It is possible that interspecific competition was a confounding variable in the observed preference for other shell types in the literature. Perhaps *P. samuelis* or even *P. granosimanus* outcompeted *P. hirsutiusculus* for *Tegula* shells in these past studies, resulting in a perceived preference for other shell types.

Proposed Work

Moving forward, it would be useful to scale up this work, increasing the number of trials and number of hermit crabs for each species tested to see whether the trends (or lack thereof) I observed in my preliminary data continue to be apparent in a larger dataset. If that is the case, I will need to determine which of my potential explanations for the observed trends in shell choice are valid. In these future trials, I will record the size of both the original shells and the final shells in order to eliminate any confounding impacts of shell size on selection. Although I attempted to use shells of roughly equal size in my preliminary experiment, it is possible that small variations in size impacted the data. I also plan to collect more shells from the less common shell types so that I can have an equal number of each shell type in the tank.

An observational survey of the shells that species occupy in the greater Pacific Grove region would also be useful as a complement to the laboratory experiments. For example, by examining the shells occupied by *P. granosimanus* in areas where *Tegula* shells are more abundant versus areas where *Tegula* shells are less abundant, I could determine whether my hypothesis that *P. granosimanus* are often found in *Tegula* shells merely because the shells are abundant is correct. I would take measurements of tidepool height, shell types available, and the shell species typically occupied by hermit crabs there. I can compare these field surveys to laboratory data to determine whether the hermit crabs simply choose the shells that are available in that particular area.

It would also be useful to conduct a number of trials in which interspecific competition is present. In these trials, hermit crabs of multiple species would be placed in the tank at the same time and the number of shells of each shell type would be more limited. Two-species trials could be used to observe the effects of competition between each pair of *Pagurus* species and three-species trials could be used to test the effects of competition between all three species simultaneously. If the results differ from the single-species trials for any of the three species, I could conclude that competition affects shell preference. If *P. hirsutiusculus* is an inferior competitor, this could explain the discrepancy between the literature and my experiment regarding their shell preferences.

It would also be informative to carry out trials in which the preferred shell species is not available to assess each species' alternative choices. This could be a useful variable in predicting the impact of any shifts in snail populations on each hermit crab species. For example, it is unclear what the second choice of *P. samuelis* would be, considering that nearly all choose *Tegula funebralis* shells. Without a suitable alternative, any decrease in *T. funebralis* population may degrade the *P. samuelis* population by making the hermit crabs more vulnerable to predation or reducing reproductive success. A decline in this ubiquitous detritivore could in turn have significant impacts on nutrient cycling in Monterey Bay rocky intertidal areas. Perhaps the other *Pagurus* species with their less defined shell preferences would be better equipped to handle changes in snail populations, and a decline in *P. samuelis* could help them thrive by reducing competition. *P. granosimanus* might benefit most, or at least be less negatively impacted by shifts in snail population than the other species due to its complete lack of shell preference.

These ecosystem effects could be investigated through a series of larger-scale and longer-duration experiments. We could continuously remove live *T. funebralis* snails as well empty *T. funebralis* shells from areas of the intertidal and observe what happens to the hermit crab population in these areas relative to control plots. If the *P. samuelis* population declines, then we would know that a decrease in preferred shell availability could negatively impact *P. samuelis* and that we should be concerned about any anthropogenically driven changes in *Tegula* populations. We could also observe the populations of the other two species in these experimental plots to see how they are impacted. If declines in *P. samuelis* do occur, we could determine whether decreases in this competitively dominant species would benefit the other two species. With this information, we will be a step closer to predicting the impacts of global change on intertidal communities.

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