

The Role of Shell Color in Visually Mediated Substrate Selection of Hermit Crabs

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ABSTRACT

Many organisms are reliant on sensory structures to be able to sense and interact with their environment. Such as in, marine invertebrates have many structures that are related to mechanoreception, olfaction, and chemosensation. Another sensory mechanism, vision, is crucial for invertebrates living in the intertidal due to rapidly changing environmental conditions. To look more closely, hermit crabs have compound eyes that allow them to see the world around them. Although past research has focused on their chemosensory abilities, increasing evidence suggests that visual cues also influence their behavior, such as predator avoidance and shell selection. This paper will evaluate if hermit crabs display a preference for different colors of sand and if they display behavior that suggests they would prefer to be on a low-contrast sand color in comparison to their already occupied shell color. Using a 1-gallon tank with split black and white sand on either side, a 10-minute experimental trial was conducted using 19 hermit crabs of the species *Pagurus granosimanus* and *Pagurus birsutiunculus*. Wilcoxon signed-rank tests revealed no significant preference for black or white sand and no significant preference for low-contrast sand relative to shell coloration. These findings suggest that substrate color alone may not be a primary factor influencing habitat selection in hermit crabs, although additional environmental cues may be necessary to elicit visually mediated habitat-selection behavior.

INTRODUCTION

Marine invertebrates rely on many different sensory structures such as antennae, statocysts, and compound eyes to interact with and respond to their environment. In intertidal habitats, where environmental conditions can change quickly due to tides, predation, and habitat complexity, the ability for organisms to sense their habitat plays a crucial role in survival. As an example, hermit crabs in particular are highly behaviorally responsive organisms that depend on environmental information to locate resources such as shells, and avoid predators (Hazlett 1981). Although hermit crabs are more commonly associated with chemosensory, increasing evidence suggests that visual cues may also contribute to habitat assessment and shell-related decision making. Studies have shown that hermit crabs can integrate visual information when evaluating potential shells and that visual cues may interact with other sensory capabilities during resource acquisition (Ping et al. 2015). Furthermore, visual information has been implicated in shell-selection decisions and camouflage-related behaviors, suggesting that hermit crabs are capable of assessing aspects of their surrounding environment through vision (Briffa et al. 2018; Wilby et al. 2018; Partridge 1980). Hermit crabs have also been shown to integrate multiple sensory modes like memory and cost–benefit evaluations when making shell-related decisions, highlighting the complexity of their decision-making beyond simple cue responses (Elwood et al. 2022). Understanding how hermit crabs respond to visual information can provide further insight into how sensory systems influence habitat selection and anti-predator behavior.

Furthermore, the hermit crab species *Pagurus bernhardus* has demonstrated the use of visual contrast to assess the effectiveness of their camouflage in comparison to their surrounding environment (Briffa et al. 2018). Individuals changed their shell selection behavior depending on the degree of contrast between their shell coloration and background color. Seemingly they preferred the least amount of contrast when choosing a shell, suggesting that their visual perception contributes to predator avoidance strategies such as camouflage (Briffa et al. 2018). Similar visual background-selection behavior has also been observed in other crustaceans, such as *Carcinus maenas* will select environments that improve camouflage (Twort & Stevens 2023). These studies suggest that substrate appearance and environmental coloration may influence habitat preference and movement behavior in hermit crabs.

Orientation studies have also shown that hermit crabs are capable of using both visual and chemical information to guide movement and environmental navigation, suggesting that visual cues may influence spatial decision making beyond shell selection (Chiussi et al. 2001; Rodríguez et al. 2023). Despite increasing evidence

that hermit crabs use visual cues to influence many of the decisions they make, relatively little research has examined whether hermit crabs use substrate color itself as a cue during habitat selection. Many intertidal habitats contain strong visual contrasts, such as dimmer environments due to coverage of algae and larger organisms or more light exposed and lighter colored areas. Preference for darker or lighter substrates may therefore reflect ecologically relevant behaviors associated with camouflage, shelter seeking, or predator avoidance. Furthermore, with potentially predators that are visually guided, it would be beneficial to be able to camouflage with the environment that a hermit crab may end up in. Additionally, understanding visually moderated habitat selection may provide more insight into how marine invertebrates balance sensory information when navigating through their environment.

This study will investigate whether adult Hermit crabs of collected *Pagurus granosimanus* and *Pagurus hirsutiusculus* prefer to reside on a darker or lighter substrate within a controlled two-choice environment. By isolating substrate color as the primary sensory variable, this study seeks to answer two questions: (1) do hermit crabs display a preference for different substrate colors, and (2) do they preferentially occupy substrates that reduce visual contrast with their shell coloration? Based on previous findings demonstrating the importance of visual cues in shell selection and camouflage assessment, I predicted that hermit crabs would spend more time on substrates that more closely matched the coloration of their occupied shell. Such behavior would be consistent with camouflage-associated substrate selection and may enhance an individual's survival.

MATERIALS & METHODS

Animal Collection and Care

19 Adult *Pagurus granosimanus* and one *Pagurus hirsutiusculus* were collected from Argyle Lagoon on San Juan Island. These individuals were selected based on size (approximately 3 centimeters long by columella length), activity, and healthy appearance (i.e., no severe damage to their shells, legs, etc.). Crabs were then brought to the lab in a bucket with their original seawater, small cobble, and algae to make their travel less stressful and to provide a familiar medium in their new lab tank. To place them in a sea-table with flowing seawater, they were all individually placed in small square containers with flow holes that were propped up in the sea-table so the containers may not fall nor be overfilled with water that would allow the hermit crabs to escape. Over the course of five days, they were fed, and the containers were cleaned every other day, as well as an algae change in each container. Each hermit crab had a label (1-20) near or on their respective container to ensure

tracking of each crab when it came to running the experiment. Additionally, hermit crab number four was removed due to its shell being too proportionally big compared to its body, ultimately affecting its sand preference. Before running the trials, I took a series of pictures of each crab in black sand and white sand (in separate containers) to be able to measure their contrast ratio between them and their chosen substrate throughout the experiment. In addition to this step, I also created labels that were in each picture that included columella length, overall color, patterns and other notes of each shell that the crabs resided in.

Experimental Procedure

In terms of the experimental setup, I obtained a small one gallon plastic tank, a stopwatch, and bought aquarium safe black and white sand. To place the sand on their respective sides in the tank, I created a plexiglass divider (unattached) that was eventually held up by the sand. After washing the sand, they were placed on one single side of the container, such that one side was only black and the other was only white (Figure 1).

To start trials, each crab was allotted a three minute acclimation period within the tank but in a holed container. This was to potentially minimize additional stress due to the change in environment. The crab was then removed from the holed container and placed on the plexiglass divider and given 10 minutes to freely roam. During the 10 minutes, I logged which sand color they were on every 30 seconds, which was kept on a stopwatch, so this provided 21 sand choices throughout the experiment. This was repeated for each crab while changing the tank water only once to avoid constantly disturbing the sand, but still to keep water somewhat fresh and without other sensory cues. Excel was used to log data including columella length and the 21 sand choices out of the trials.

Statistical Analysis

Total count on black sand and white sand was calculated for each individual hermit crab; using this, a total count of black and white sand choices was grouped together. To help answer the question if the hermit crabs preferred a low contrast sand color, I calculated a contrast ratio between the shell color and both sands. Using ImageJ, I found the means of luminance of shell color and sand, then used the Michelson Contrast calculation to compute the ratios between the means. This provided two values for each hermit crab, one for contrast on black sand and one for white sand (Figure 2). These values were then compared, the higher value corresponds to the higher contrast value and the smaller value corresponds to the low contrast value. Whichever was the higher value (i.e., black or white sand), the count from that category was used as the count for the high

contrast count. Similarly for low contrast, whichever sand color had the lowest contrast value, that count in that category was used for the low contrast count.

Then, with these values, in RStudio, I did two Wilcoxon signed-rank tests for statistical analysis, one to compare just sand color, and two to compare high and low contrast. These findings will ultimately highlight if hermit crabs use visual cues during habitat selection, in which individuals are expected to preferentially orient toward and spend more time on one substrate type that matches more closely with their shell color.

RESULTS

To address the two research questions, two paired Wilcoxon signed-rank tests were conducted. The first test evaluated whether hermit crabs exhibited a preference for black or white sand substrates. No significant difference was detected between the number of observations on black and white sand (Wilcoxon signed-rank test, $p = 0.778$, $V = 87.5$, $n=19$, Fig. 3). As shown in Figure 3, counts on black and white sand were similar, with substantial overlap in the distributions and variation among individuals.

The second test looked into if hermit crabs were on substrates that produced lower visual contrast with their occupied shell. Similarly, no significant difference was found between observations on high-contrast and low-contrast sand (Wilcoxon signed-rank test, $p = 0.386$, $V = 73$, $n=19$, Fig. 4). Figure 4 shows that observations were distributed across both contrast categories, with overlapping interquartile ranges and no clear preference for either treatment.

Overall, neither substrate color nor substrate-shell contrast significantly influenced substrate occupancy in the hermit crabs *Pagurus granosimanus* and *Pagurus hirsutiussculus* under the conditions of this experiment.

DISCUSSION

The results of this study did not support the hypothesis that hermit crabs would preferentially occupy substrates that matched the coloration of their occupied shell. No significant preference was detected for black versus white sand substrates ($p = 0.778$), nor was there evidence that hermit crabs preferentially occupied low-contrast substrates relative to their shell coloration ($p = 0.386$). Although previous research suggested that visual information can influence camouflage-related behavior in hermit crabs, the present study indicates that substrate color alone may not strongly influence habitat occupancy under the conditions tested.

These findings differ from studies that have demonstrated visually induced camouflage assessment in hermit crabs. Wilby et al. (2018) found that *Pagurus bernhardus* preferentially selected shells that reduced visual contrast with their surrounding environment, suggesting that hermit crabs can assess camouflage using visual cues. Likewise, Rimmer et al. (2021) reported that visual information can influence shell-selection behavior under certain contexts. Based on these studies, it was predicted that hermit crabs would similarly favor substrates that reduced visual contrast between their shell and the environment. However, no such pattern was observed in this experiment. This inconsistency suggests that the visual structures involved in shell selection may not necessarily extend to habitat or substrate selection.

One possible biological explanation is that shell choice and substrate choice differ substantially in their importance. Gastropod shells provide direct protection from predators, desiccation, and physical disturbance, making shell selection a high-value decision for hermit crabs (Hazlett 1981). In contrast, substrate color may contribute less to survival because the shell itself already provides a substantial degree of protection. As a result, hermit crabs may invest more effort into selecting an appropriate shell than selecting a substrate that improves camouflage. If this explanation is correct, visual assessment of camouflage may occur primarily when acquiring a shell rather than during simply inhabiting an environment.

Another possibility is that substrate color alone does not accurately represent the complexity of natural habitats. Intertidal environments contain a mixture of rocks, algae, and variable lighting conditions. In nature, hermit crabs may respond to combinations of visual cues rather than substrate color in isolation. For example, darker substrates may only become advantageous when paired with structural cover, reduced predator exposure, or other environmental characteristics. The absence of a preference in this study may therefore indicate that substrate color is only one component of a more complex habitat-selection process. Additionally, the observed variation among individuals may also provide insight into the results. While some crabs spent substantially more time on black sand and others spent more time on white sand, no consistent population-level pattern emerged. Such variation may reflect differences in previous life experience, shell condition, shell species, or individual behavioral tendencies.

Although the hypothesis was not supported, the results contribute to a broader understanding of sensory ecology in hermit crabs. Previous studies have established that hermit crabs can use visual information when assessing shells and camouflage opportunities (Wilby et al. 2018; Rimmer et al. 2021). The present study suggests that the use of visual cues may be context-dependent, with certain decisions relying more heavily on visual information than others. Additional experiments would be useful for determining whether visual cues

influence habitat selection under different ecological contexts. One approach would be to expose hermit crabs to a predator and see whether substrate preferences become stronger under perceived predation risk. If camouflage is important primarily as an anti-predator strategy, substrate matching behavior may only emerge when predation risk is elevated. Future studies could also incorporate different types of substrates such as rocks, algae, and varying light levels to better mimic environmental conditions encountered in the field. Finally, larger sample sizes and a broader range of shell colors may help determine whether certain shell types exhibit stronger background-matching behavior than others.

Overall, this study found no evidence that hermit crabs preferentially selected substrates based on color or shell-substrate contrast. While these results did not support the original hypothesis, they suggest that substrate color alone may not be a primary factor influencing habitat occupancy. Instead, visually assisted behaviors found in previous studies may be more closely associated with shell selection or may require additional environmental cues before influencing habitat choice.

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FIGURES

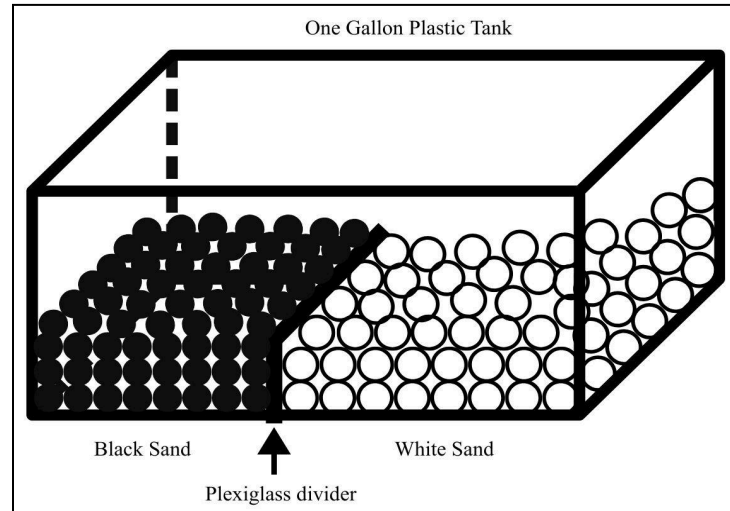


Figure 1: Drawing of Experimental setup. One gallon plastic tank was used for the experiment, with one half of the tank filled with white sand and the other half filled with black sand. These were divided by a plexiglass divider that was unattached and just held up by the weight of the sand. No alterations or changes were made to the sides in which the colors of sand were in throughout the experiment.

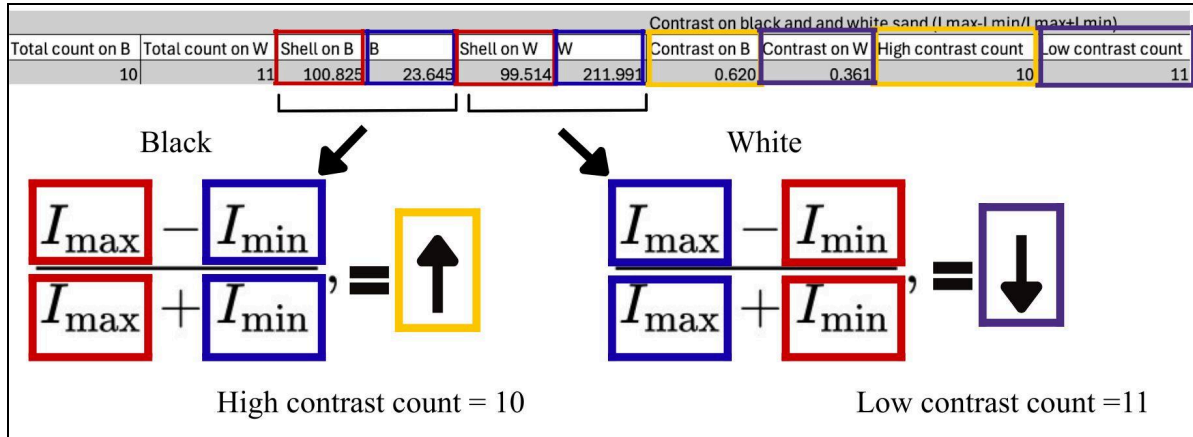


Figure 2: An example of how high and low contrast sand counts were determined. Each crab (row) had its own high contrast count and low contrast count. In other words, how much time did it spend on the high contrast sand versus the low contrast sand in comparison to their shell color. The columns “shell on B” (shell luminance on black sand), “B”(luminance of black sand), “shell on W” (shell luminance on white sand), and “W” (luminance of white sand) were the values of mean luminance found using ImageJ. These were then plugged into the Michelson contrast formula (shown above). The output was “Contrast on B” and “Contrast on W”. These two contrast ratios were then compared and determined which one was high contrast (high value) and low contrast (smaller value). The total counts of time spent on black sand and white sand were then translated respectively to either high contrast count or low contrast count.

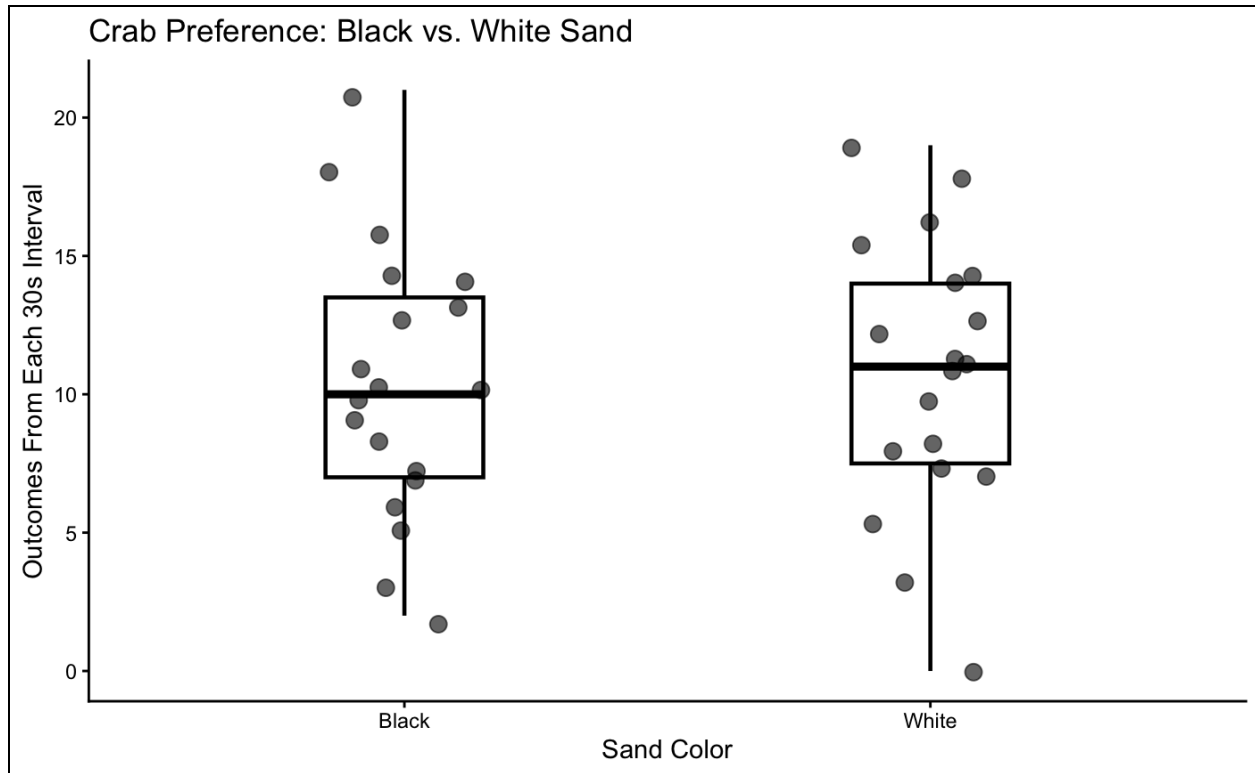


Figure 3: Comparison of counts on black and white sand with each individual crabs graphed during the 10 minute trial period. $p\text{-value} = 0.778$ and $n=19$. Where the left box is counts spent on black sand, and the right box is counts spent on white sand throughout the trial. The means of both sand color counts are near 10, meaning crabs usually spent nearly 50% of their time on either sand color.

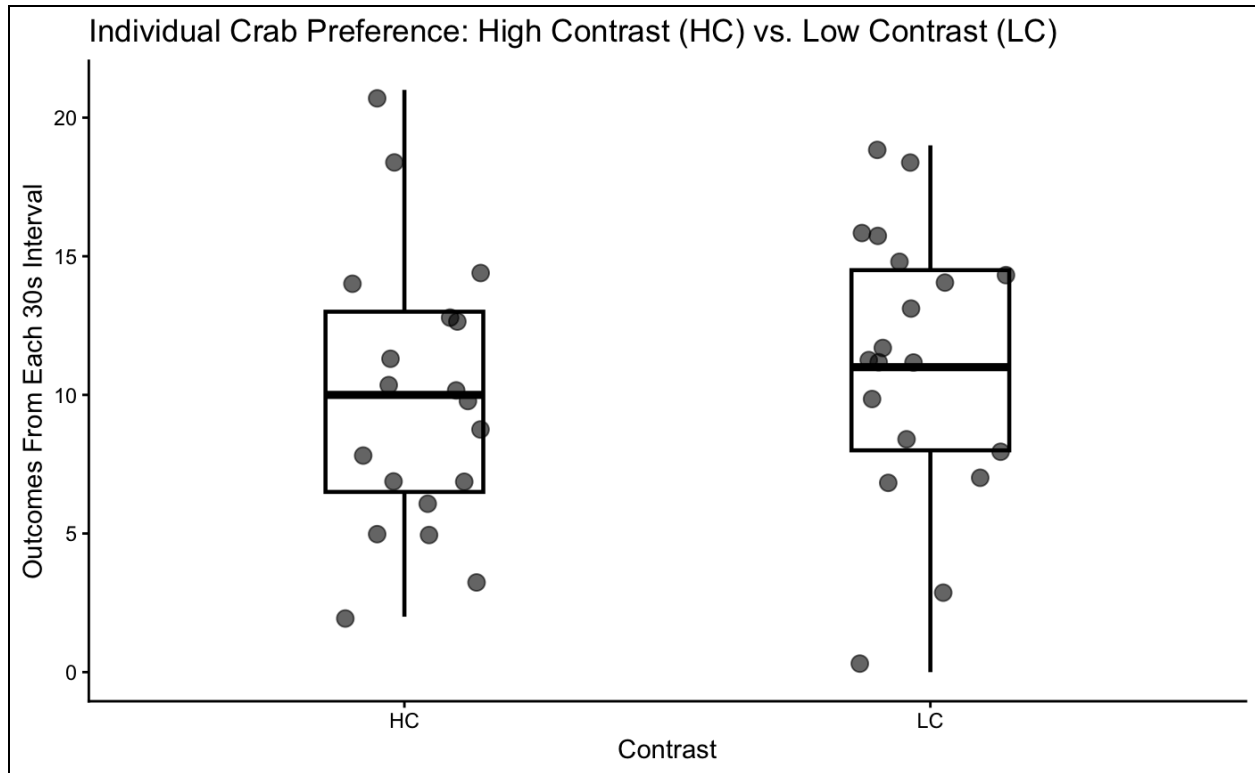


Figure 4: Comparison of high contrast count and low contrast count with each individual crab graphed during the 10 minute trial period. $p\text{-value} = 0.386$ and $n=19$. Where the left box represents counts on high contrast sand and the right box reveals counts on low contrast sand out of their experimental trial. Both boxes are relatively near 10, meaning the hermit crabs spent half their time on both sands. Although low contrast count is slightly higher than high contrast sand, demonstrating slightly more counts or time spent on low contrast sand.