

Hermit crabs as a model for resource distribution and acquisition in social groups

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ABSTRACT

Resource inequality is a pervasive and pressing issue affecting the well-being of individuals in societies around the world. Multidisciplinary researchers have previously utilized economic, sociological, and anthropological lenses to understand why and how inequality spreads in populations. However, recent studies have proposed that the distribution of shell resources in hermit crabs may be affected by factors analogous to those affecting the wealth distribution curves of human populations, indicating a potential for the use of hermit crabs in investigating resource inequality through a behavioral and biological lens. Building upon these studies, the effect of individual behavior, group size, and social interactions on the heterogeneity of resources in groups of terrestrial hermit crabs was examined. Crabs were placed in situations with varying levels of social interaction and their behavior observed and recorded. A distribution of initial shell resources was compared to that of shell resources following exposure to various levels of social interaction. Preliminary data indicates that crabs that change their shells tend to move into larger shells, and that shell switches tend to increase the Gini coefficient, a measure of resource inequality, of the sample group regardless of the allowed level of social interaction. Through this study, a foundation for understanding the effect of individual behavior, social interactions, and group size on the acquisition and distribution of resources, as well as an examination of the applications and limitations of utilizing hermit crabs as a model for studying resource distributions in human populations, will be formed.

INTRODUCTION

Animal models have been used broadly to study the development of individual behavior and response since the late 19th and early 20th century (Tully, 2003) and have since expanded to investigate the social interactions between dyads and multiple members of populations (Dugatkin, 2002, 2007, 2017; Lewis et al., 2014; Brent, 2015). The similarities between the social behavior of humans and non-humans allows for the investigation of social phenomena through animal models (Chase et al., 2020; Sokolowski, 2010). A working definition of social behavior focuses on the effect of these interactions within groups and the influence of group experiences on individual behavior (Sokolowski, 2010). In both humans and non-humans, these social behaviors often arise within a broad, interconnected network of social ties (Brent, 2015). Understanding the impacts of interactions between individuals in social groups on behavior is an important step toward understanding social phenomena in animals and, by extension, human populations.

Traditionally, much research in the field of animal social behavior has focused on interactions between mammalian or vertebrate species. However, the use of simpler model organisms, especially in the study of large-scale social phenomena, has the potential to provide new possibilities in sociological, biological, and behavioral research. In particular, hermit crabs have been identified as a such potential model system. Previously, hermit crabs have been used to study a wide variety of topics, from the effect of sensory input on social dynamics (Steele and Laidre, 2019; Tidau and Briffa, 2019) to resource partitioning and risk-taking decision-making (Alcaez et al., 2020; Billock and Dunbar, 2011). Recently, hermit crabs have been identified as a potential model for resource inequality in human

populations due to their social behaviors and ownership of scarce, discrete, and quantifiable resources in the form of their shells, which bears much similarity to the use and movement of housing in human populations (Billock and Dunbar, 2011; Laidre, 2011, 2019; Chase et al., 2020). The snail shells used by hermit crabs as shelter and protection can be obtained through taking the shell of a recently-deceased snail, fighting other hermit crabs for their shells, or through vacancy chains, a social structure describing how discrete, reusable, and limited resources move through populations (Chase et al., 1988; Kehle and Rotjan, 2009; Lewis and Rotjan, 2009). These vacancy chains, also observed in human resource distribution, occur when a hermit crab switches shells, causing a series of sequential shell switches follows where other crabs move into newly-vacated shells until the last shell discarded is of such low quality that no crab moves to claim it. Rotjan et al. 2010 identify two types of vacancy chains: synchronous, where several crabs queue by a vacant shell in descending order, then rapidly exchange shells once a suitable crab moves into the vacant shell; and asynchronous, where a solitary crab switches into a vacated shell, leaving behind its own discarded shell for another crab to find later (Rotjan et al., 2010).

Recent findings on hermit crab resource distribution and acquisition indicate that social structures and interactions similar to those found in human populations, such as vacancy chains, may have a profound effect on the distribution of resources in crab populations (Chase et al., 2020). In Chase et al.'s 2020 study, the first description of inequality in material resources in a population of hermit crabs was presented. From a sample of hermit crabs observed from the wild, it was found that the shell resource distribution, using shell dry weight as the measure of value, appeared to resemble the

wealth distribution curves of human societies more than they resembled theoretical curves based on purely ecological forces like survival, growth, and mortality, suggesting that the distribution of shell resources in hermit crab populations may be influenced by factors analogous to those affecting wealth inequality in human populations (Chase et al., 2020).

Building upon Chase et al. 2020's study, a small-scale pilot study was performed to investigate hermit crabs' potential as a model organism for studying the effect of social interaction on the distribution of resources in populations in a controlled, experimental setting. In this study, three levels of crab group size (individual – 1 crab per compartment, dyad – 2 crabs per compartment, or group – 6 crabs per compartment) and two levels of line of sight (restricted or unrestricted) were used. The initial and final average shell opening diameter and average shell weight were recorded and analyzed for all trials were investigated. Further, the change in Gini coefficient, a gauge of economic inequality, was investigated for resource distributions created from multiple sample study trials. Impacts on crabs' shell exploration and switching behavior, as well as behavior regarding other crabs and the study environment, were studied using video footage taken during the experiments. Finally, an ANOVA analysis was used to further explore the potential impact from interaction of crab group size and line of sight on final shell opening diameter or shell weight, besides potential impact from individual factors, such as crab group size and line of sight.

METHODS

Thirty terrestrial hermit crabs (*Coenobita clypeatus*) were purchased from Carolina Biological Supply Company. Three tanks were set up with several centimeters of play sand substrate, a hygrometer, a tank heater, a digital camera, and three plastic dishes for food, freshwater, and saltwater as living habitats for hermit crabs. The crabs were given Florida Marine Research hermit crab food and dechlorinated freshwater and saltwater twice a day. Tanks were heated to 80 degrees Fahrenheit using a Lowes pipe warmer for a heating strip, and humidity was raised to 70% through moist sand and OURRY Mushroom mini-humidifiers from Amazon. The tanks were placed by a window, allowing for natural lighting. The crabs were allowed a two-week adjustment period prior to beginning study trials. Crab behavior during this period of adjustment and all study periods was monitored through observation and camera footage.

Two hundred natural silver-mouthed turban shells (turbos) were purchased from Atlantic Coral Enterprise. Seventy-eight of these shells were selected and categorized with their weights and opening diameter. The turbo shells used in this study had circular apertures ranged from approximately 23 millimeters to 33 millimeters in diameter and weights ranging from approximately 26 grams to 77 grams.

The shells were inspected and intact shape and then boiled in dechlorinated water to remove any potential hazards. Shells were randomly selected for experimental use, then prepared by submerging in a baking soda and dechlorinated water solution (1 teaspoon baking soda to 1 cup of water for 8-9 cups to water) for ten minutes or until bubbles formed, drained, then submerged in 1% sea salt solution (20 g salt for 2000 g dechlorinated water) or until bubbles formed, and last rinsed with dechlorinated water for 10 minutes. All water

used was boiled and then dechlorinated prior to use with two drops of Seachem Prime water conditioner per four liters of water. This process was undertaken to clean the shells and imitate the state of shells recently washed up on the shore, as adapted from web source “How to Choose Hermit Crab Shells: The Best Sizes and Shapes,” recommended by an online hermit crab care forum. Since the majority of shells sold in pet stores are bleached, baking soda was used to neutralize any potential remaining bleach residue to minimize harm to the hermit crabs.

Two study arenas were created for running simultaneous trials. Each arena was made of plastic and spanned 65.4 by 46.7 by 18.1 centimeters with several centimeters of play sand substrate. Study arenas were then divided into smaller compartments of six, two, or none using divider sets of clear plastic or wood, with each compartment having one, two, or six crabs, depending on the treatment, maintaining roughly the same square area per crab across the treatments. In order to reduce the human observations on disturbance of hermit crabs, the whole process was recorded to replace human observations each 10-30 minutes.

The effect of varying levels of social interaction on hermit crabs’ choice to switch into shells and the resulting distribution of shell resources in the group, as represented by shell weight and opening diameter, was investigated by conducting choice tests with crabs under different treatments of social interaction. Two types of social interaction were examined: group size with three levels (individual – 1 crab per compartment, dyad – 2 crabs per compartment, or hexad – 6 crabs per compartment) and line of sight with two levels (restricted or unrestricted). The study arena for group size = 1 trials was divided into

six compartments with one crab and two shells placed in each compartment, and the study arena for group size = 2 trials was divided into three compartments with two crabs and two shells placed in each compartment (see Figure 1). Sight restricted trials utilized compartment dividers made of wood, and sight unrestricted trials utilized compartment dividers made of clear plastic so as to preserve the crabs' line of sight for crabs and shells in neighboring compartments. For group size of 6 crabs, six crabs and three shells were placed in the arena. The group size of 6 arenas did not have dividers and all crabs in the trial were able to see and physically interact with all other crabs, and no sight restricted test was performed. Each experimental setting was conducted on at least 3 different dates with at least 18 crabs in total tested. The diagrams of the three group size study arenas are illustrated in Figure 1 and the experimental design in Table 1. To give crabs some recovery time, the experiments were performed with at least one day of rest between trials.

Shell 1a	Shell 2a	Shell 1b	Shell 2b	Shell 1c	Shell 2c
Crab A		Crab B		Crab C	
Shell 1d	Shell 2d	Shell 1e	Shell 2e	Shell 1f	Shell 2f
Crab D		Crab E		Crab F	

Study Arena for Individuals (group size = 1)

Shell 1a		Shell 1c		Shell 1e	
Shell 2a		Shell 2c		Shell 2e	
Crab A	Crab B	Crab C	Crab D	Crab E	Crab F

Study Arena for Dyads (group size = 2)

Crab A	Crab B		Crab C	
Shell 1		Shell 2	Shell 3	
Crab D	Crab E		Crab F	

Study Arena for Groups (group size = 6)

Figure 1: Diagrams of study arenas for the three different group sizes (1, 2, and 6).

Dividers are indicated in bold.

Table 1: Chart showing breakdown of treatments in the study where n is the number of compartments, depending on the treatment.

Individual		Dyad		Group (6)
Sight Restricted	Sight Unrestricted	Sight Restricted	Sight Unrestricted	Sight Unrestricted
Compartments=6	Compartments=6	Compartments=3	Compartments=3	Compartments=1

(Each experimental setting was conducted on at least 3 different dates with at least 18 crabs tested)

In each trial, randomly selected hermit crabs were placed into study compartments containing 2-3 randomly selected shells. Study trials lasted three hours. The initial and final shell identification number, weight, and opening diameter were recorded, as well as crab interactions with the study environment, shells, and other crabs; crab size; and the physical position of the chosen shell relative to the crab.

After the trials, videos of each trial were analyzed for crab interaction with shells, other crabs, and the study environment, as characterized by crabs antennating each other, crabs antennating shells (exhibiting interest in shells), crabs switching into shells, crabs climbing compartment walls (exhibiting exploratory behavior), or crabs burrowing into the ground (exhibiting avoidance behavior). Crab behavior was recorded at intervals of five minutes throughout the videos.

RESULTS

Impact on shell resource distributions

To investigate the potential changes on shell weight and size after shell changes, the initial and final average shell opening diameter and average shell weight were recorded and analyzed for all trials and for trials in which the crabs changed shells. The average final shell opening diameter and average final shell weight appeared to be larger than the average initial shell opening diameter and average initial shell weight, indicating that when crabs switched, they tended to switch to larger shells in either weight or size. However, because this change was small and the standard error was relatively large due to the small sample

size of hermit crabs used, the only change in initial and final opening diameter or weight that was significant was the change in opening diameter (Figure 2a) and shell weight (Figure 2b) for changed trials.

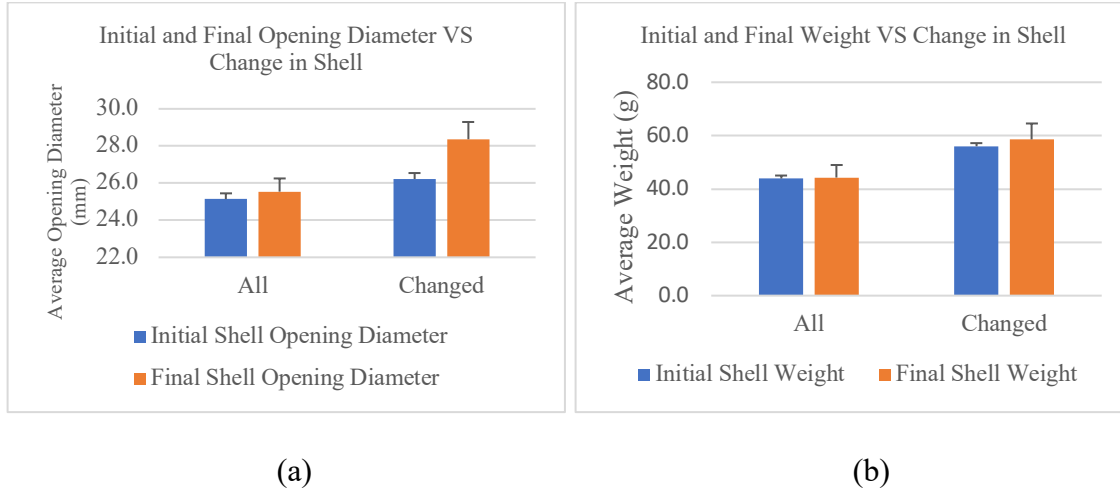


Figure 2: (a) Initial and final opening diameter for all shells and changed shells; (b) Initial and final weight for all shells and changed shells

The Gini coefficient is a statistical measure of the distribution of a variable in a population. It is often used as a gauge of economic inequality, measuring income distribution across populations. The coefficient ranged from 0 (0%) to 1 (100%), where 0 is perfect equality and 1 is perfect inequality. In this study, the Gini coefficient for several populations of crabs derived from the sample studied was calculated and compared with the coefficient before and after shell switching using the following formula (Davidson 2010).

$$G = 1 - \frac{2}{\mu} \int_0^{\infty} y(1 - F(y))dF(y)$$

In all cases except for the distribution of shell weight for the group size of 6, the Gini coefficient increased between the beginning and the end, suggesting that the shell switching—in particular, switching into larger shells—leads to an increase in the Gini coefficient, which is in line with the consideration of how the Gini coefficient is calculated (Figures 3 and 4). If most crabs do not switch shells but some switch into larger shells, as was seen in most cases of switching, then the distribution of shell wealth would become more uneven throughout the population, leading to a larger Gini coefficient. However, in previous observational studies of hermit crab resource distributions in the wild, the Gini coefficient was not found to be extremely high, indicating that there are factors, perhaps such as death of crabs leading to larger shells becoming available, that stop the Gini coefficient from continuously increasing.

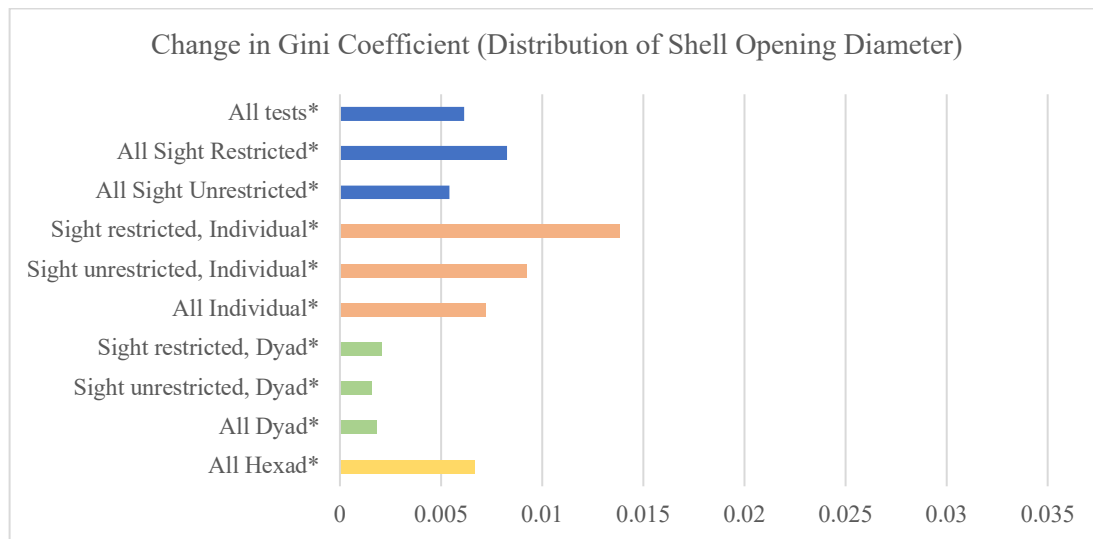


Figure 3: Change in Gini coefficient for shell opening diameter in resource distributions created from combined trials

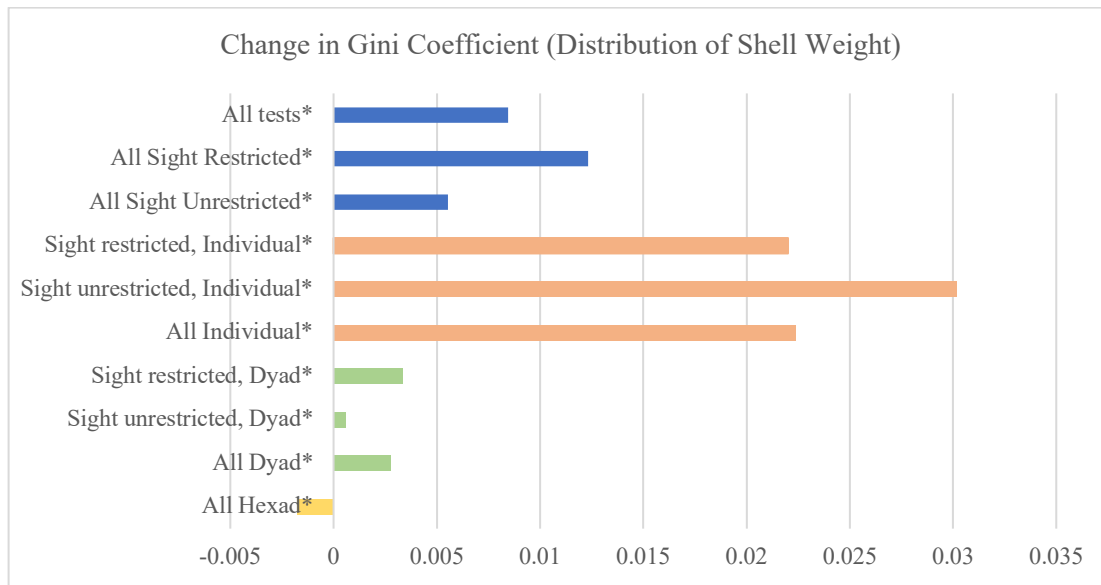


Figure 4: Change in Gini coefficient for shell weight in resource distributions created from combined trials

In both the resource distributions using shell opening diameter and shell weight, the increase in the Gini coefficient between the initial and final distributions was greatest for the individual (group size = 1) group as compared to other levels of group size, and increased the least in the dyad (group size = 2) group, regardless of the crabs' allowed line of sight. In almost all cases, the increase in the Gini coefficient for distributions with sight restricted was slightly larger compared to distributions with sight unrestricted, indicating that the resource distribution may be affected by crabs being able to sense other another. This indicates that the physical and sensory presence of another crab in the trials may have affected the crabs' shell resource distributions, possibly through affecting the crabs' shell-switching behavior. However, the relationship between groups of different levels of group size and the changes in the Gini coefficient between the initial and final distributions did

not seem to be consistent through all group sizes, as the change in the Gini coefficient for the cluster hexad group (group size = 6) was not observed to follow the same pattern of more group members leading to less change in the Gini coefficient, as was expected after comparing the change in the Gini coefficient for the individual group and the dyad group. This may suggest that the influence of other crabs beyond the dyad may not be as strong, or that crab behavior regarding shell resources may differ in dyad vs. larger social group situations. However, the change in the Gini coefficient was small in most cases and, as the result, the standard deviation of the Gini coefficients was relatively large, so these differences were not significant.

Impact on crabs' interaction with shells and switching behavior

An indication of change and crab identification number was plotted in Figure 5. The graph indicated that shell switching was a rare event, potentially due to the vulnerability inherent in switching shells, as indicated by most crabs only changing once or twice, though certain crabs appeared to change multiple times throughout their trials (Figure 5). The graph also indicated that some crabs were tested more times than others. This may have been due to some crabs being removed from the sample through death or molting.

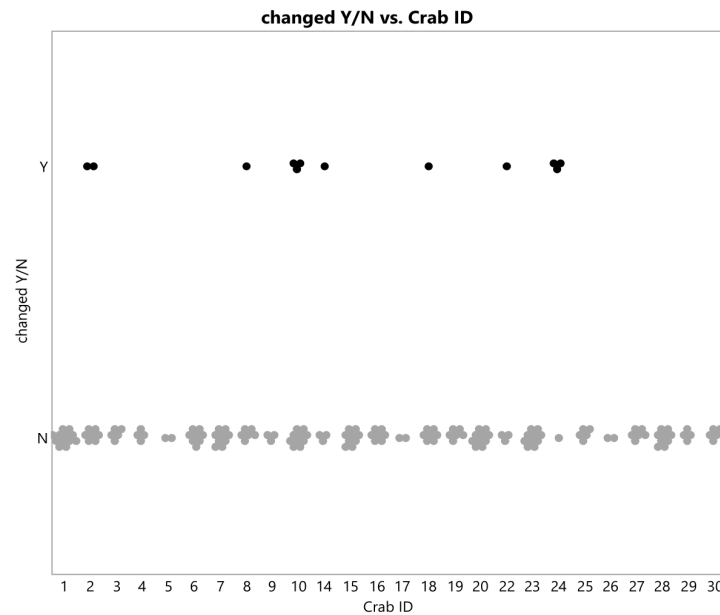


Figure 5: Graph of change indicator (y/n) by crab identification number

To further evaluate the potential social interaction during the study period, all shell changes and crab-shell interactions during each study period were reviewed and analyzed for all the groups. Although a larger proportion of crabs with line of sight unrestricted exhibited interest in shells compared to the proportion of crabs with line of sight restricted that exhibited interest in shells, a larger proportion of crabs with line of sight restricted actually changed into another shell compared to the proportion of crabs with line of sight unrestricted that actually changed into another shell. However, the p-value (calculated using the formula for p-value for difference in proportions) is large for both columns, so the differences were not significant.

During the review of video footage, it was observed that crabs could change into a new shell and change back to their original shells later. In addition, a crab could also

change back and forth to a new shell multiple times before deciding whether to take the new shell. Therefore, studies were done to investigate the number of crabs which made shell switches during the 3-hour study time frame and compare 1) the proportion of crab that were interested in a new shell, identifying as contacting/investigating the shells, during the 3-hour study time frame over the total crabs, and 2) the proportion of crab that made shell switches during the 3-hour study time frame over the total crabs at different experimental setting. In Individual trials, no significant differences were found between sight restricted vs sight unrestricted on proportion of crabs that are interested in a new shell (65.2% vs 77.8%, $p=0.19$), proportion of crabs that made shell switching (21.7% vs 11.1%, $p=0.18$) or proportion of crabs that climbed (34.8% vs 22.2% $p=0.19$). In addition, in individual group setting, no crab burrowing was observed. Furthermore, in dyad trials, although still no significant differences were found between sight restricted vs sight unrestricted in the proportion of crabs that are interested in a new shell (62.5% vs 45.8%, $p=0.12$), however, proportion of crabs that made shell switching (25.0% vs 8.3%, $p=0.06$) or proportion of crabs that climbed (37.5% vs 4.2% $p=0.01$) or proportion of crabs that burrowing (8.3% vs 29.2%, $p=0.03$) were significant at $p=0.1$ level (Figure 6), indicating group sizes, maybe crab-crab interaction could impact crab behaviors including shell switching.

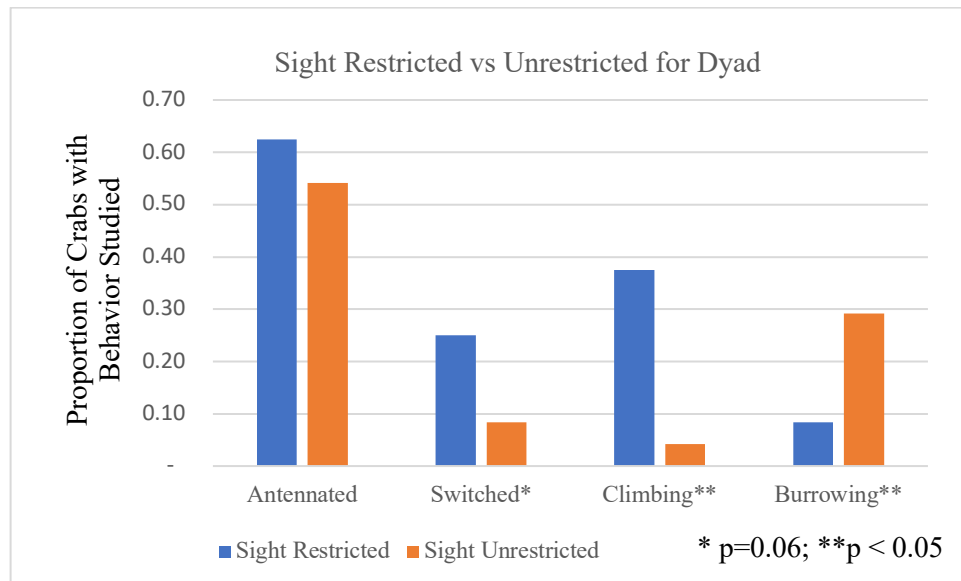


Figure 6: Graph of crabs that exhibited interest in shells and that changed shells between restricted and unrestricted sight groups for Dyad trials

Figure 7 shows with significance that shell switching happened more often for the group of six crabs than other group sizes over the observation period of 3 hours of each test, while the numbers of the final switching are comparable across all groups. This indicates that in the group setting, shell exploration and interaction happen more often, while the final decision may not change the overall number of shell switches.

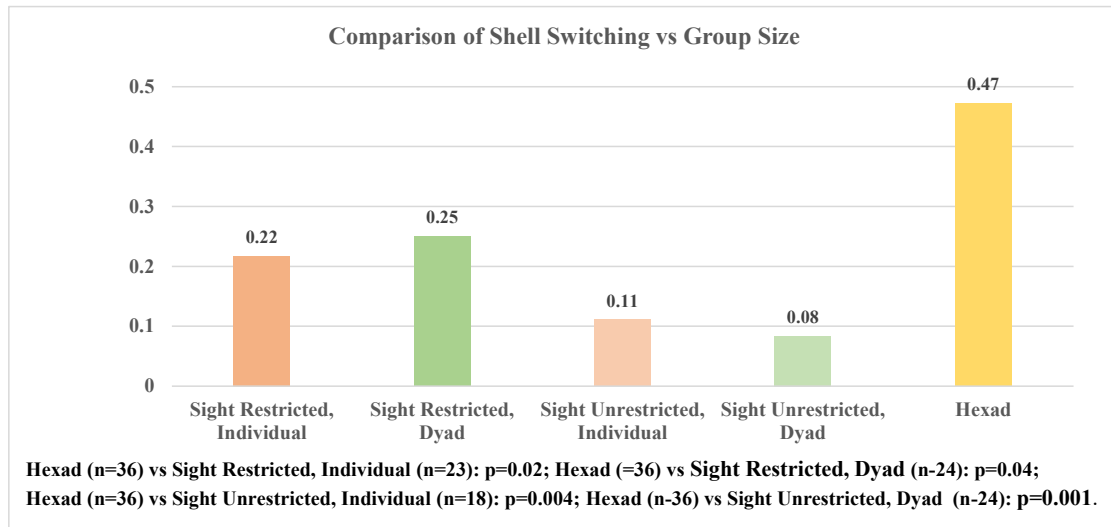


Figure 7: Proportion of shell switching for all group sizes

Investigating factors impacting the final morphology of the shells occupied

As a further analysis, an analysis of variance (ANOVA) was performed for all trials to investigate relationships between response (i.e. final shell opening diameters or shell weight) and explanatory variables (i.e. different levels of experiment settings), especially whether interaction between the explanatory variables may have impact on response variable. In the analysis, two main categorical explanatory variables were used: 1) shell changes (changed or not changed), and 2) line of sight (sight unrestricted or sight restricted).

First, an ANOVA including a term for the interaction of shell change and line of sight was performed to investigate the potential impact of two main explanatory variables and their interaction on final shell opening diameters. As showed in Table 2, no significance is shown for the cross term, indicating that there does not appear to be a

significant cross interaction between shell change and line of sight regarding to their impact on the mean of the final opening diameter. However, shell changes indicated having significant impact on the mean of the final opening diameter.

Table 2: ANOVA of final opening diameter, with shell change and line of sight as separate explanatory variables with cross interaction

Analysis of Variance					
		Sum	of	F	Prob >
Source	DF	Squares	Mean Square	Ratio	F
Model	3	221.3027	73.7676	4.2756	
Error	153	2639.7303	17.2531		
C. Total	156	2861.033			0.0063*
Sight	1	0.074981		0.0043	0.9475
Changed	1	85.413352		4.9506	0.0275*
Changed*Sight	1	34.603835		2.0057	0.1587

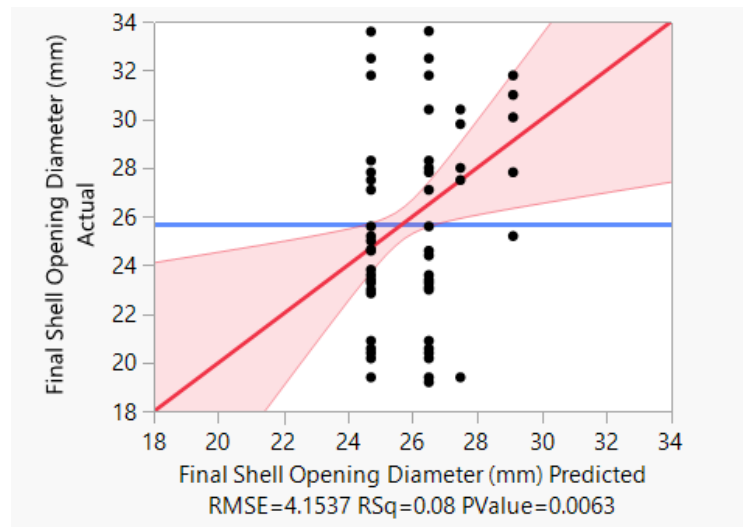


Figure 8: ANOVA of final opening diameter, with shell change and line of sight as separate explanatory variables with cross interaction

Since the interaction of two explanatory variables aren't significant, another ANOVA was performed with two main explanatory variables to identify their independent impact on final shell opening diameter. Table 2 shows that the difference in the mean of the final opening diameter between shell changed vs unchanged as well as in sight restricted vs unrestricted were both significant, further solidifying that crabs tended to change into shells with larger opening diameters. In addition, line of sight also seems to have an impact on the final opening diameter, with the sight restricted group having a larger mean of the final opening diameter when considered separately.

Table 3: ANOVA of final opening diameter, with shell change and line of sight as separate and independent explanatory variables

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Model	2	173.6446	86.8223	4.9789	
Error	153	2668.0001	17.4379		
C. Total	155	2841.6447			0.0080*
Sight	1	88.737658		5.0888	0.0255*
Changed	1	76.4552		4.3844	0.0379*

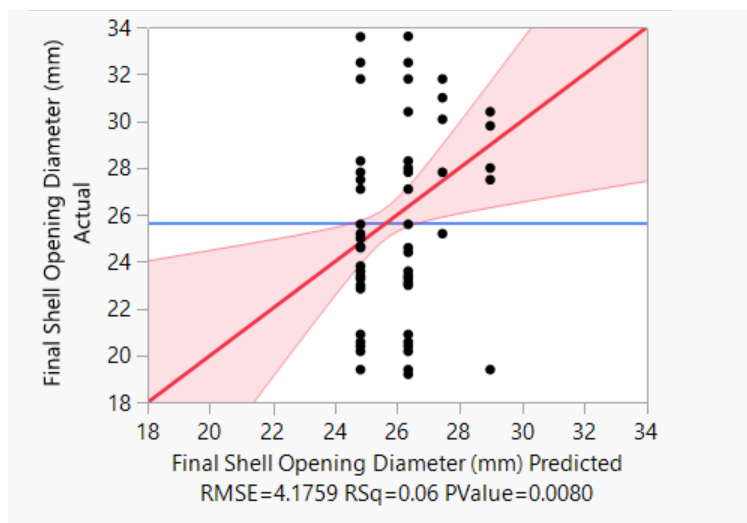


Figure 9: ANOVA of final opening diameter, with shell change and line of sight as separate and independent explanatory variables

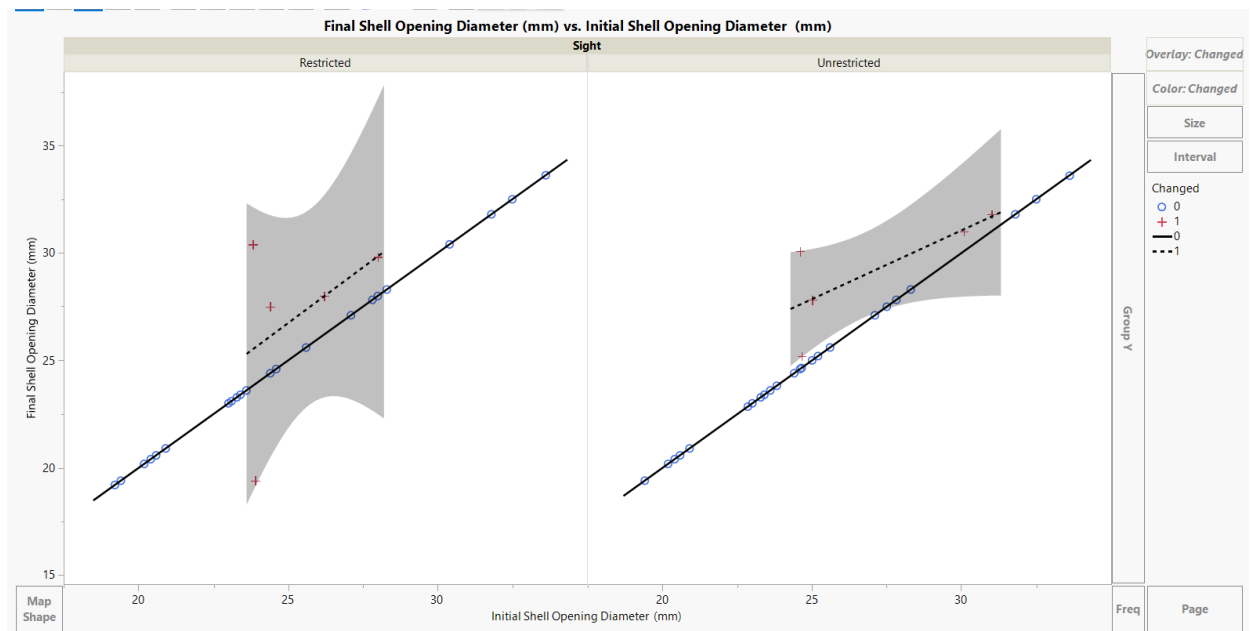


Figure 10: Graph of final shell opening diameter vs initial shell opening diameter, color-coded by an indicator of change (1 = change, 0 = no change) and grouped by line of sight (restricted and unrestricted)

Similar ANOVA analysis was performed on final shell weight as response variable with two main explanatory variables, an indicator of shell change (changed or unchanged), and line of sight (sight unrestricted or restricted). The ANOVA results indicated that interaction isn't significant on final shell weight. When investigating shell changes and line of sight as two independent explanatory variables (Table 4, Figure 11) the shell change shows a significance while the line of sight does not. This indicates that the mean of the final shell weight is impacted by shell changes, but not the line of sight. Therefore, unlike the final shell opening diameter, the final shell weight appeared to differ between crabs that changed shells and crabs that did not change shells, with a larger final shell weight

mean in crabs that did change shells. However, line of sight did not appear to have a significant relationship with final shell weight.

Table 4: ANOVA of final shell weight, with shell change and line of sight as independent explanatory variables

Analysis of Variance					
Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Model	2	2560.272	1280.14	6.0035	
Error	152	32411.063	213.23		
C. Total	154	34971.334			0.0031
Sight	1	426.6414		2.0008	0.1593
Changed	1	2039.5663		9.5651	0.0024*

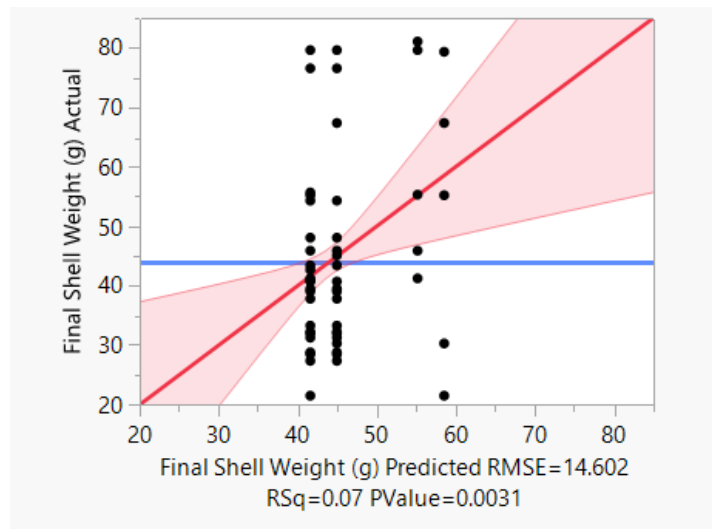


Figure 11: ANOVA of final shell weight, with shell change and line of sight as independent explanatory variables

In summary, crabs that changed their shells tended to move into larger and heavier shells, and that shell switches tended to increase the Gini coefficient of the sample group regardless of the allowed level of social interaction. The data also suggest that the crab identification number may be associated with shell change, and sight appears to be a minor contributor to shell switching.

CONCLUSIONS AND DISCUSSION

As previous literature indicated that crabs may have a preference for certain properties of shells, such as opening shape and opening diameter, it was determined that one type of shell would be used for all tests in this study to reduce this potential confounding factor (Turra and Leite1, 2003; Domincianoa et al.. 2009). In addition,

previous experience with shells has been documented to influence hermit crabs' future shell selection (Turra and Leite¹, 2003; de Meireles et al., 2008). As the crabs ordered from Carolina Biological came with West Indian Topshell (*Cittarium pica*) shells, which are very thick and heavy with oval openings and a somewhat low conical form, the shell selected for use in this study was the silver-mouthed turbo, a similarly thick and heavy shell with a round opening, as well as the closest type of shell to the West Indian Topshell able to be purchased in bulk and in various sizes. In future studies, different shell species, such as West Indian Topshell (*Cittarium pica*), *trochiform*, and *turbiniform*, could be tested to find the most preferred shell types of the hermit crabs being studied, so shell preference wouldn't be a potential factor in influencing crab decisions on shell changes.

In this study, hermit crabs were successfully used to study the effect on social interactions on resource distribution in a controlled, experimental setting. However, several limitations arose, such as the small sample size of crabs. Additionally, what hermit crabs perceive as a more "valuable" shell remains an unclear subject, as growing hermit crabs are different sizes and thus search for different shells that "fit" them, so there is no fixed value for the best shell for a hermit crab at every point in its life. However, the finding that most crabs that changed shells changed into wider-apertured, heavier shells seems to corroborate the current belief that shells with larger weights and larger opening diameters are more valuable to hermit crabs. Though, in this study, most hermit crabs chose to not switch into a larger shell when given the choice; some crabs were even observed to switch into larger shells and then switch back. Further studies could potentially shed more light

on the mechanisms of value in hermit crab shells, whether there even is a universal property deemed more valuable for all hermit crab shells beyond fit, and if different species of hermit crabs value different shell properties. Because resource distributions and the Gini coefficient utilize one measure of value in their quantification of wealth inequality, understanding what makes one shell more valuable to a crab over another may lead to a better ability to use hermit crabs as models for studying resource distribution and inequality.

As no synchronous vacancy chains were observed but there were still instances of crabs switching shells and the Gini coefficient increasing, it is likely that factors other than the specific social structure of vacancy chains have effects on the distribution of resources in hermit crab populations. For example, individual differences in behavior—some crabs were observed to actively attempt to switch into shells both in the study arena and in the habitat, whereas other crabs were consistently less zealous. Other social interactions such as crabs fighting with each other over shells, marked by the lack of a vacant shell for a crab to move into, were observed in the habitat, indicating that there may be exchange of shell resources occurring in dyad behavior. More study is needed to investigate the impacts of these individual and dyad behaviors on the overall distribution of resources in groups of hermit crabs.

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