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Fiddler Crabs and Selfish Herds: High School Cliques or More Diverse?

Shelby Warrelmann

Marsh fiddler crabs (*Uca pugnax*) have diverse foraging habits which are dependent on the personality of each crab. The formation of droves or preference to scavenge alone may correspond to factors such as: Location within a herd, herd size, size of males, and feeding rate. Previous research suggests that 1) a central location in a herd corresponds to an increase in feeding rate 2) herd size doesn't affect feeding rates and 3) location within a herd often is related to an individual's size. A multi-year observational study was conducted to determine the validity of these claims and found that while some of these assertions were supported, others lacked any sort of statistical support.

Shelby Warrelmann is a senior at Coastal Carolina University. She has been a member of the College of Science Research Fellows since freshman year and will be finishing her undergraduate degree in marine science in December. Her study of the behaviors of marsh fiddler crabs was conducted under the guidance of Eric Rosch, professor in the Department of Marine Science.

Introduction

The theory of the selfish herd is one that has been heavily researched in a variety of species in birds, fish, and mussels. It theorizes that as individuals become more centralized in a herd, they are offered more protection from predation. This however comes with a reduction in the availability of food. As a result, individuals must make the choice to risk exposure to predation for more plentiful food or remain safe but compete for food. Waving in fiddler crabs is a courtship and territorial behavior, which is demonstrated by crabs regardless of the presence of females (Pope, 2000).

Fiddler crabs tend to forage in two styles dictated by their individual crab personalities. These variances in exploratory activity can be linked to an individual's location in a herd or drove, or their preference to remain mostly alone. Individuals were classified as outgoing based on a tendency to avoid herd activity and explore on their own. Shy individuals tended to cluster together in herds and droves (Knotts and Griffen, 2016). A drove – large feeding group, can sometimes fragment into a smaller herd upon the approach of a predator. These herds are referred to as “selfish miniherds” (Viscido and Wethey, 2002). The fragmentation of a drove into selfish miniherds only occurs as a last resort when the crabs cannot find safety before the predator is upon them (McLain et al., 2015).

There are three observations which are expected according to the previously mentioned existing data which pertain to a variety of herds. The first is that males in the center of the herd (CM) feed more often than those on the outside of the herd (PM's) and more than individuals not in any herd (IM's). The second is that herd size does not seem to have a major effect on the feeding rate. The third is that centrally located males tend to be large or medium but are rarely small, and PM's tend to be medium or small.

Currently, there is a large amount of information dealing with selfish herds in various species such as birds and fish. There is, however, a lack of information focusing on fiddler crabs. This experiment aims to fill the gap in the fiddler crab research pertaining to the “selfish” herds theory among fiddler crab populations.

Methods

For the purposes of the experiment, herds have been defined as individuals who are clustered together and move as a cohesive group. Herd size was broken into five categories: extra-small herds are comprised of fewer than 6 individuals, small herds are 6-10 crabs, medium herds are 10-14 crabs, large herds are 15-19 crabs and extra-large herds are 20 or more crabs. Feeding is classified by movements of the major or minor claw from the ground to the mouth of the crab. Waving is measured as one back-and-forth claw movement over the head and body of the crab. Physical size of each male is determined by sight, though on average fiddler crabs are about 20 mm in length.

To reduce the impacts of human presence on the crabs, binoculars or a spotting scope were used to observe behaviors.

Once a herd was selected, a central male and peripheral male were selected. For each of these males the feeds and waves per minute, and the size were recorded. This information was also collected for individual males. Data were collected from crabs at Waties Island, Huntington Beach State Park, and Sanford Cox Sr. Community Park. These areas were chosen because of their relatively low levels of human activity. The collected data were then compiled and analyzed in a variety of implications to determine the validity of the current observations regarding fiddler

crabs. Data have been collected by multiple researchers over various periods of time, beginning in 2016.

Results

Impact of Location on Feeding

In order to streamline data from crabs that are exceedingly energetic or lethargic, feeds per minute and waves per minute were calculated as a percentage of total actions. The total actions taken by all crabs of each type (CM, PM, or IM) were determined along with the percentage of those actions which were feeding actions and waving actions. Central males were found to devote 93.31% of their actions to feeding and 6.69% of their actions to waving. Peripheral males were found to devote 95.82% of their actions to feeding and 4.78% of their actions to waving. Independent males were found to devote 93.02% of their actions to feeding and 6.98% of their actions to waving (Fig. 1 and Fig. 2).

Impact of Herd Size on Feeding

The average waves per minute and feeds per minute were calculated for each herd size by taking the average of all such actions for each crab in each sized herd, regardless of crabs location within the herd.

In extra small herds an average of 2.6 waves per minute and 50.5 feeds per minute was found. Central males were found to have an average amount of waves per minute of 2.4 and 54.7 feeds per minute. Peripheral males were found to have an average of 2.8 waves per minute and 45.7 feeds per minute (Fig. 3).

Small herds were found to have an average of 3.2 waves per minute and 50.9 feeds per minute. Central males were found to have an average of 4.2 waves per minute and 57.0 feeds per

minute. Peripheral males were found to have an average of 2.1 waves per minute and 45.8 feeds per minute.

In medium herds an average of 2.9 waves per minute and 59.7 feeds per minute were present. Central males were found to have an average of 3.4 waves per minute and 58.8 feeds per minute. Peripheral males were found to have 2.5 waves per minute and 60.5 feeds per minute.

Large herds were found to have an average of 14.6 waves per minute and 44.0 feeds per minute. Central males were found to have an average of 19.6 waves per minute and 57.1 feeds per minute. Peripheral males were found to have an average of 9.1 waves per minute and 53.6 feeds per minute.

In extra-large herds an average of 3.2 waves per minute and 36 feeds per minute were discovered. Central males were found to have an average of 2.2 waves per minute and 37.0 feeds per minute. Peripheral males were found to have an average of 4.2 waves per minute and 35.5 feeds per minute.

Independent males were found to have an average of 3.2 waves per minute and 31.4 feeds per minute. The trendline depicting the waves per minute across the herd sizes has an R^2 of 0.1452 and $y = 1.2554x + 1.5444$. The trendline depicting the feeds per minute across the herd sizes has an R^2 of 0.4147 and $y = -3.5874x + 58.972$.

An ANOVA test comparing the correlation between herd size and feeds per minute returned an F value of 11.3 and a non-significant p-value (Fig. 4). A second ANOVA test comparing the correlation between herd size and waves per minute returned an F value of 9.4 and a non-significant p-value (Fig. 5).

A post hoc test of wave rate and feed rate in relation to herd size revealed the significances and non-significance between each size grouping (Fig. 6).

Relation of Location and Size

Of the central males 62% were large, 37% were medium, and 1% were small. Peripheral males were found to be 20% large, 60% medium, and 20% small. Of individual males 33.33% repeating were found to be large, 53.33% repeating were found to be medium, and 13.33% repeating were found to be small (Fig. 7).

Discussion

Impact of location on feeding

While it was expected that central males would feed more than peripheral males and independent males, the percent of feeding action for each group is roughly the same as is the percent of waving action for each group. This disproves what was originally expected. Peripheral males were found to have a higher percent of feeding actions than central males and individual males. This indicates that in the fiddler crab system the theory that the center of a herd will be more devoid of food than the edge of the herd may be untrue. The feeding and waving patterns of individual crabs tend to be most similar to the patterns of central males.

Impact of herd size on feeding

The line depicting the waves per minute across herd sizes indicates a decent bit of overlap present between independent males and males in a herd. The positive slope of the trendline of the waves per minute across herd size line indicates a positive correlation between herd size and feeds per minute. The negative slope of the trendline of feeds per minute across herd size indicates a negative correlation between herd size and feeds per minute. The line depicting the average amount of feeds per minute of herded males does not overlap with the average feeds per minute found in independent males. However, the information supported by

both trendlines is irrelevant due to the ANOVA Tests. Both ANOVA tests returned F values that were higher than the P-value, indicating the F is not significant and therefore that herd size has no correlation on feeds per minute or waves per minute.

A post hoc test of the wave rate present for each herd size, including independent crabs revealed fewer non-significance between groups than a post hoc test of feed rate present for each herd size. The post hoc test for wave rate depicts non-significance between large sized herds and each of the other herd sizes; independent, extra-small, small, medium, and extra-large. The post hoc test for feed rates depicts non-significance between independent crabs and extra-small, small, medium, and large herds, between extra-small herds, independent crabs and extra-large herds, between small herds independent crabs and extra-large herds, between medium herds independent crabs and extra-large herds, between large herds independent crabs and extra-large herds, and finally between extra-large herds extra-small, small, medium, and large herds.

Relation of Location and Size

The data supported the expected ratios of sizing corresponding to each crab type. The data also indicated that independent males had sizing patterns most similar to peripheral males. This is contrary to what was observed of the crab's behavior in the feeding actions.

Conclusion

While the claims that herd size was not correlated to feeding rate and that central males and peripheral males had specific sizes was supported, one claim was not. The original claim that central males have more feeds per minute than peripheral males and independent males was not supported by the data provided. Thus, further investigation of this is recommended in order to either support the findings based on the data or the literature claims. Data used in this study were

collected by many people over a long period of time, which could have introduced inconsistencies when it came to interpreting behavior. This lack of consistency created one possible area of error: determination of crab size by sight from a distance. Due to the possible area for error that this created, it is recommended that for future experiments a unified method is decided upon. This study was limited geographically to the three field sites discussed above. Additional observations may introduce other trends or behaviors. Observations of other populations of fiddler crabs, or other species may reveal different behaviors. This study is significant in that it attempts to fill the gap in the current knowledge known about fiddler crabs and their behavior as a selfish herd.

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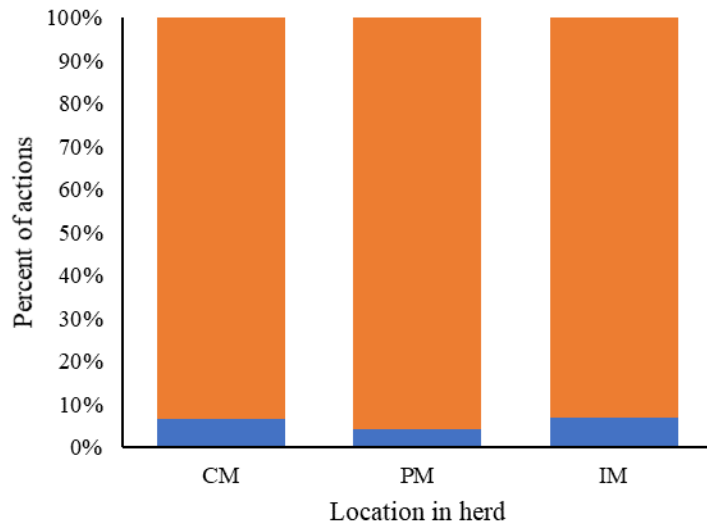
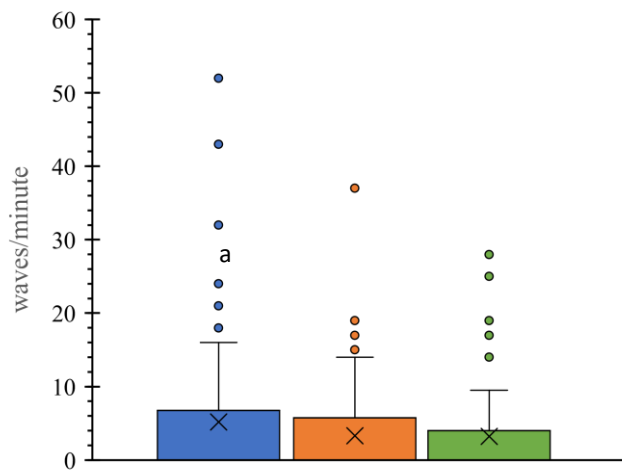
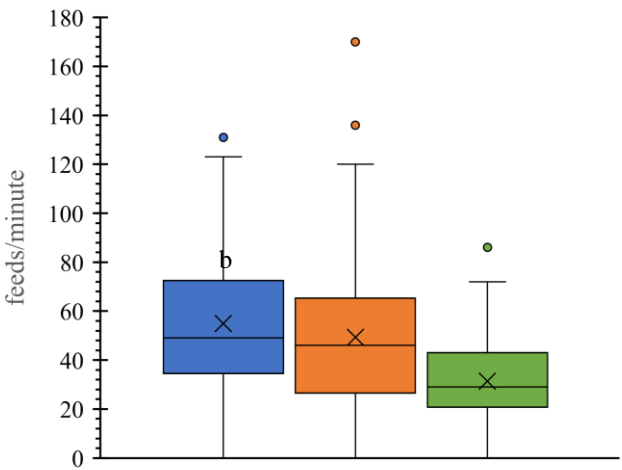


Figure 1: Graph displaying the average percent of each type of actions for each crab position. Blue represents the percent of total actions that are waves. Orange represents the percent of total actions that are feeding.



location in herd



location in herd

Figure 2: Box and whisker plot depicting the waves(a) and feeds(b) per minute of CM's(blue) PM's(orange) and IM's(green). Outliers appear along with the mean indicator and mean line in each box.

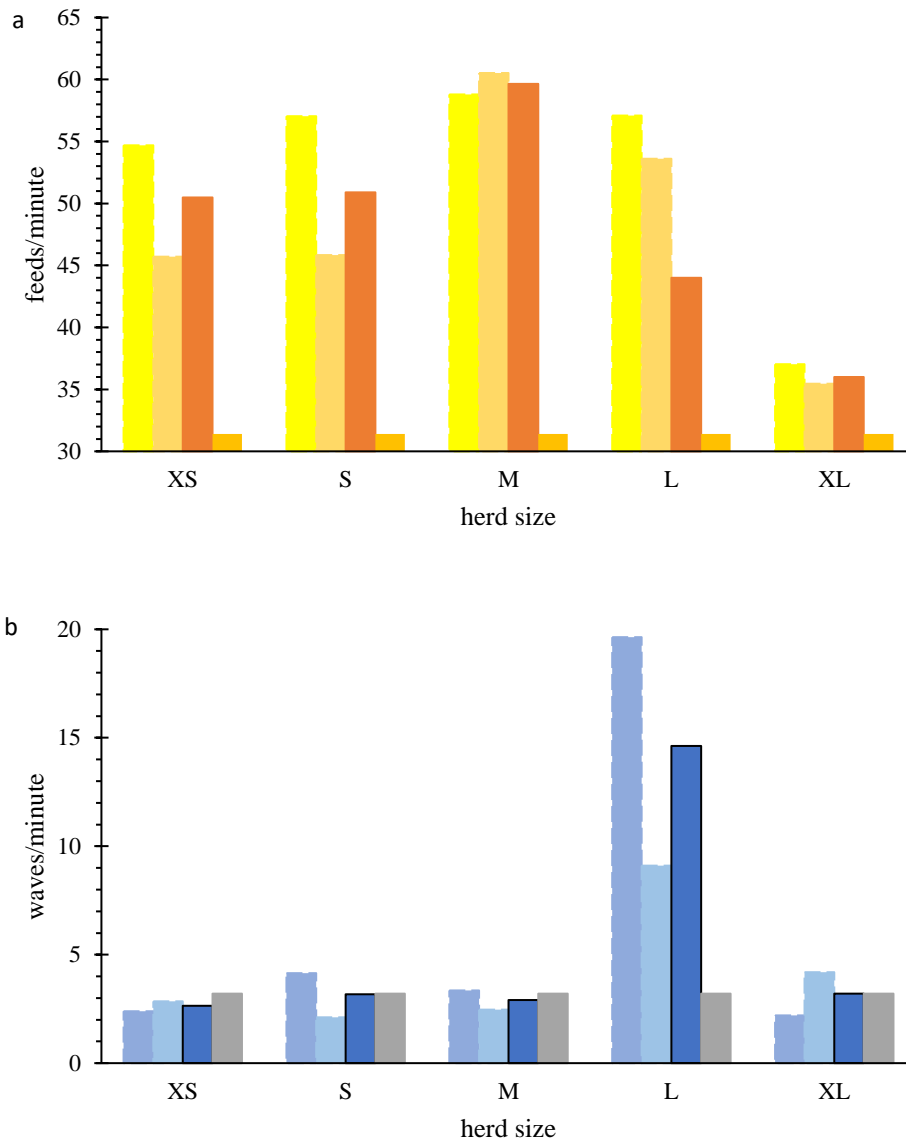


Figure 3: Bar graph depicting the average number of feeds per minute(a) and waves per minute(b) for cm's (pale blue and bright yellow) and PM's(light blue and light orange) as well as the averages for each herd size as a whole regardless of location in herd (dark blue and dark orange) compared to individual male waves(grey) and feeds(light orange).

Anova: Single Factor

SUMMARY				
<i>Groups</i>	<i>Count</i>	<i>Sum</i>	<i>Average</i>	<i>Variance</i>
XS	64	3231	50.48438	903.2378
S	53	2698	50.90566	546.1929
M	79	4713	59.65823	950.7727
L	32	1757	54.90625	827.8942
XL	35	1260	36	653.6912
I	74	2320.5	31.35811	258.894

ANOVA						
<i>Source of Variation</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	38525.91	5	7705.182	11.27227	4.73E-10	2.241261
Within Groups	226255.8	331	683.5522			
Total	264781.7	336				

Figure 4: Single factor ANOVA test comparing the correlation of herd size and feeds per minute.

Anova: Single Factor

SUMMARY				
<i>Groups</i>	<i>Count</i>	<i>Sum</i>	<i>Average</i>	<i>Variance</i>
XS	53	140	2.641509	83.7344
S	44	140	3.181818	33.79175
M	56	163	2.910714	31.31916
L	21	307	14.61905	148.0476
XL	10	32	3.2	20.4
I	54	174	3.222222	41.37421

ANOVA						
<i>Source of Variation</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	2600.759	5	520.1519	9.378535	3.73E-08	2.252955087
Within Groups	12867.17	232	55.46195			
Total	15467.93	237				

Figure 5: single factor ANOVA test comparing the correlation of herd size and waves per minute.

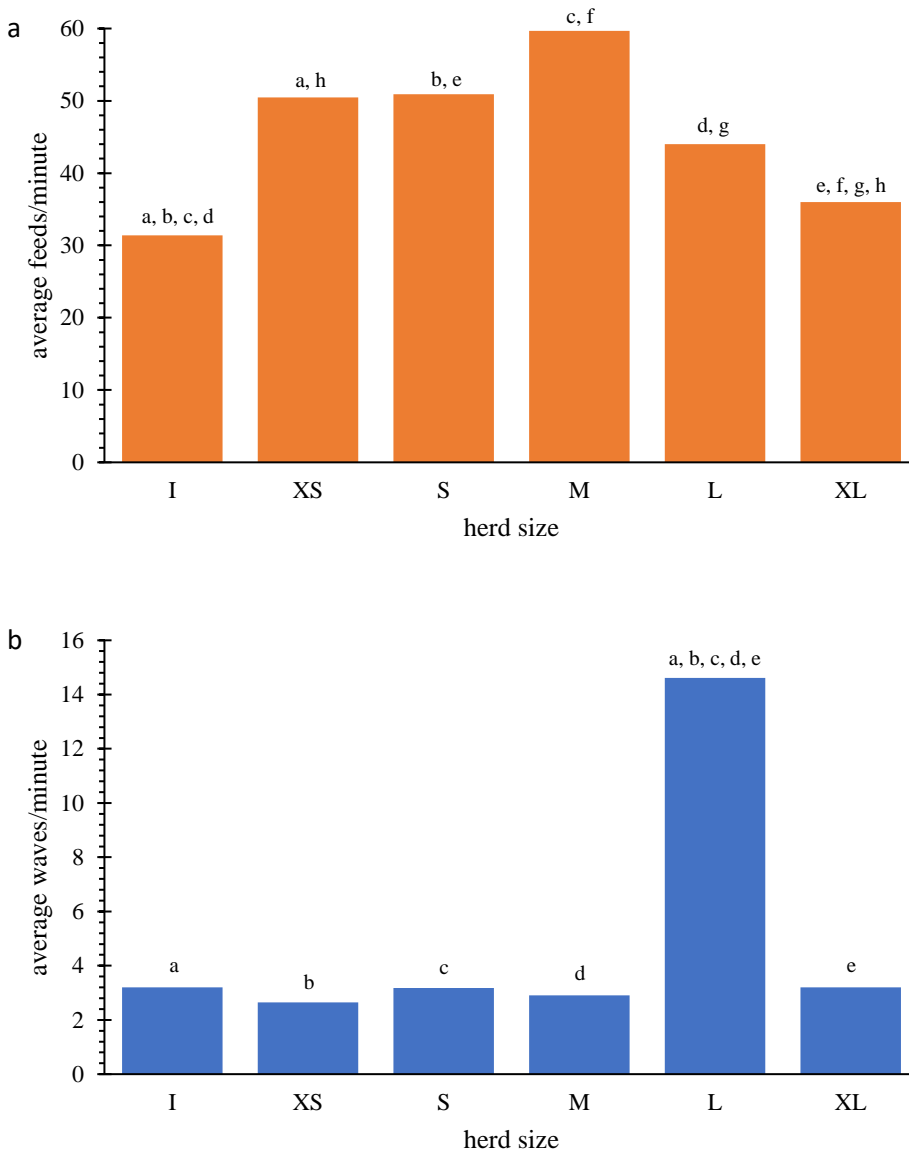


Figure 6: Bar graph depicting the average number of feeds/minute(a) and waves/minute(b) for each herd size as a whole regardless of location in herd as well as averages for independent crabs, as well as non-significances indicated by a post hoc test.

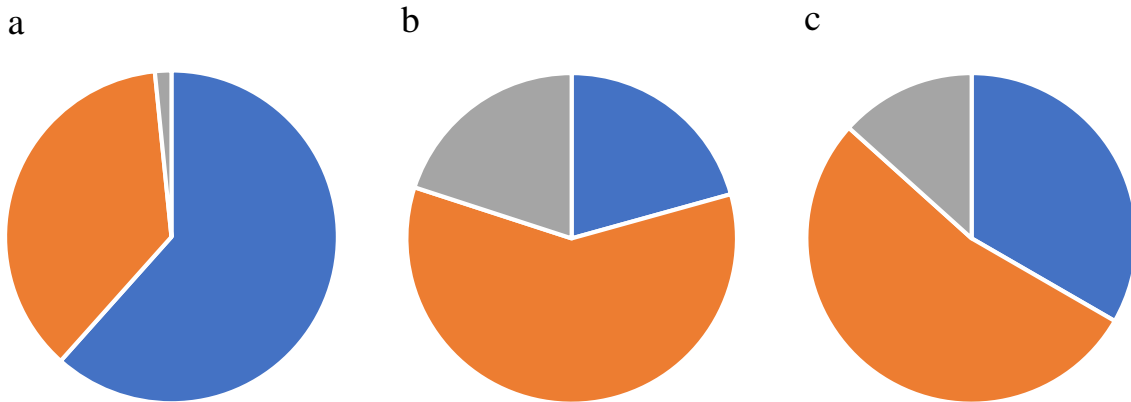


Figure 7: graphs visually depicting the percentage of each size class present at each position – central male(a), peripheral male(b), and individual(c). Large crabs are indicated by blue, medium crabs orange, and small crabs are grey.