THE EFFECTS OF DENSITY ON INTRASPECIFIC AGGRESSION IN THE FIDDLER CRAB, *UCA CRASSIPES*, ON MO'OREA, FRENCH POLYNESIA

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Abstract. *Uca crassipes* (Adams and White 1848) is one of two species of fiddler crabs found on Mo'orea, French Polynesia. Much like other animal populations, *U. crassipes* is subject to density dependent processes, such as competition, which increase with density. To better understand the relationship between competition and density, this study first looked at habitat differences between 8 distinct populations of *U. crasspies* on Mo'orea. It then explored differences in aggressive interactions between crabs at one high-density and one low-density site. In the field, both male and female fiddler crabs were found to fight more in the high-density population. Subsequent investigation of the effect of density on aggression in laboratory settings did not yield significant results. Though laboratory results were not significant, trends in data showed more fighting under high-density conditions. Further investigation is necessary to fully understand the effects of density dependent processes on fiddler crabs in both a field and laboratory setting.

Key words: Uca crassipes; *fiddler crab; density dependence; competition; aggression; Mo'orea, French Polynesia*

INTRODUCTION

Regardless of the number of offspring produced, long established populations tend to remain constant in number. This is due to environmental carrying capacity, which limits the number of individuals each environment can support sustainably over time. When populations are established in a new environment, they may grow rapidly at first, though individuals may be so widely spaced that they rarely encounter one another. As population size increases, so does the density of individuals within a specific area. When this happens, processes such as territoriality, competition for resources, emigration, and accumulation of waste generally increase as well (Raven and Johnson 1989). These processes act to regulate and reduce the density of a growing population. Within animal populations, intraspecific competition between individuals for necessary resources is the most common means of regulation (Nicholson 1954).

Fiddler crabs provide an easily observable example of density regulation via intraspecific competition. They are an abundant genus of crabs that can be found in both temperate and tropical regions around the world. Fiddler crabs are burrowing crabs that tend to live in large mixed-sex and mixed-age groups in mangrove habitats, mudflats, and other coastal muddy substrates (Bihler 2005). The crabs focus their activity around their burrow, which serves as both a mating site and a refuge from predators and the elements (Hyatt and Salmon 1978).

Fiddler crabs get their name from the male's enlarged claw, which can be up to a third of the crab's total body weight. The males use this oversized claw to attract females for mating and to threaten or fight other males. It has been shown that males increase the frequency of their waving when females are closer, meaning that the crabs are capable of accurately judging the distance of conspecifics (How et al. 2007). This ability appears to be useful in territorial defense as well since displaying males defend their territory more energetically as an intruding crab gets closer (Zucker 1974).

Fights between male fiddler crabs are usually ritualistic in nature and occur most often between crabs in adjacent burrows. Combat in male fiddler crabs has been studied intensively, and as many as 21 individual combat acts have been identified for various species (Hyatt and Salmon 1978). Male crabs fight over the best territories from which to court females. Though preferences vary between species of fiddler crab, shore level, substrate composition, temperature, organic matter content, and salinity are all thought to be important factors in burrow selection (Koch et al. 2005).

Two species of fiddler crabs (*Uca tetragonon* Herbst 1790 and *Uca crassipes* Adams and White 1848) are present on the island of Mo'orea, one of the Society Islands within French Polynesia. The two species, like other fiddler crabs, are largely associated with mangroves, although they can also be found in mudflats and other muddy terrain on Mo'orea (Bihler 2005). Though both species have been found on the island, *U. crassipes* is much more common, and many populations of the species exist around the island (pers. obs.).

The goal of this study was first to examine differences in habitat between 8 populations of the fiddler crab species *Uca crassipes* on Mo'orea and to subsequently determine whether males in a more densely populated environment exhibited more fighting behaviors than those in a less dense population. In addition to male-male fights, it has been suggested that high density increases male-female aggression (deRivera et al. 2003). Similarly, female-female aggression has been observed in some species of fiddler crabs, but it is classified as "uncommon" behavior and not much is known about it (Crane 1975, Yamaguchi and Tabata 2005). For those reasons, male-female and female-female fighting frequencies were also observed. Based on the expected increase in competition with higher density, I hypothesize that male-male, male-female, and female-female fights will all increase with higher fiddler crab densities.

MATERIALS AND METHODS

Study sites

This study utilized data from eight sites on the island of Mo'orea, French Polynesia (Fig. 1). The first four sites are drainage ditches and stream banks located along the east side of Cook's Bay. Site 1 is a drainage ditch next to the Mo'orea Pearl Resort (S 17°28'53.8", W 149°48'16.1"). Sites 2 and 3 are stream bank sites, the first adjacent to the General Assurances sign in Maharepa (S 17°28'58.0", W 149°48'36.4"), and the second just up the street from the Salon de Thé (S 17°28'59.8", W 149°48'41.6"). Site 4 is another drainage ditch between two private residences just north of Allo Pizza(S 17°29'33.4", W 149°49'01.8"). Sites 5 through 8 are mudflat and mangrove sites at different locations around the island. Site 5 is the Temae mudflats (S 17°28'42.7", W 149°46'40.9"), 6 (S 17°33'20.9", W 149°52'28.8") and 7 (S 17°33'18.3", W 149°52'43.1") are sites near the Haapiti sign, and site 8 (S 17°29'30.9", W 149°53'23.7") is a mangrove swamp just east of the Intercontinental Hotel (formerly the Beachcomber).

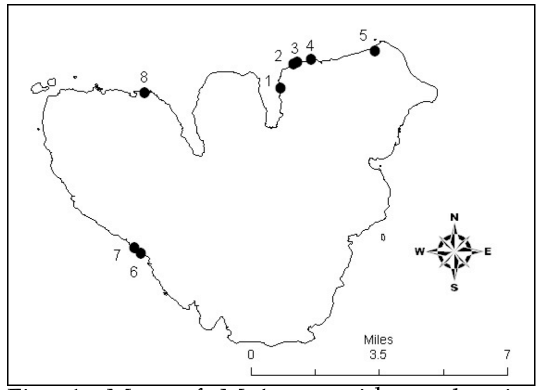

Fig. 1. Map of Mo'orea with study sites marked by numbered dots. Image based on those found in the Geospatial Innovation Facility, University of California, Berkeley.

Preliminary sediment samples were taken at each of the study sites to determine soil composition, however, no consistent differences were observed between samples from high-density sites and those from low-density sites. All 8 sites were similar in that they had the largest percentage of sediment in the 500 um size class (Fig. 2).

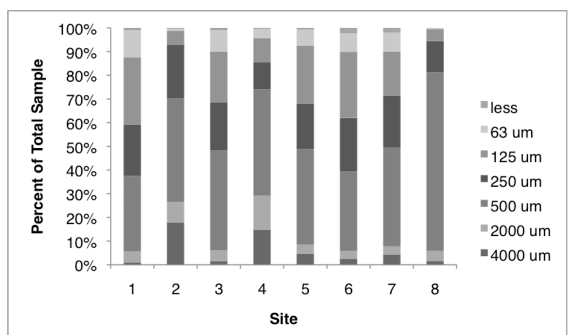

Fig. 2. Representation of the make-up of sediment samples at each field site. Samples were dried, weighed, and shaken through 6 nested sieves, resulting in the 7 size classes listed above. Each subsample was weighed to determine the percent of the total sample weight present in each size class.

Habitat Comparison

Each site was sampled with 5 randomly placed .25 m^2 quadrats. Within each quadrat the number of fiddler crab burrows was recorded to represent density, and one burrow was randomly selected to make a nearest neighbor measurement. Nearest neighbor measures were taken from the edge of the randomly selected burrow to the edge of the closest neighboring burrow. One water sample was also taken from each site. Water samples were analyzed using a refractometer to measure salinity in parts per thousand. Measurements were taken three times per sample and then averaged to ensure an accurate salinity reading.

Field Observations

The initial 8 study sites were lumped into two categories and classified as either high-density or low-density after habitat comparison samples were collected. Sites 1-4 had the highest density readings, and sites 5-8 had the lowest density readings. Further observations were then taken at 2 study sites, one high-density and one low-density. Site 1, near the Mo'orea Pearl Resort, represented the high-density site, and site 5, the Temae mudflats, represented the low-density site.

Five random 0.25 m^2 quadrats were selected at each site and aggressive interactions between crabs were recorded. For each quadrat the number of male-male, male-female, and female-female aggressive interactions were recorded over a period of 20 minutes. After initial observations, aggressive interactions were defined as threat waves between male crabs, rapid advances between crabs that resulted in physical contact, any physical contact that involved the use of a male's major claw, and quick jabs between crabs using their legs to make contact (most commonly observed in female-female aggression). The number of times two individuals were engaged in any aggressive interaction was recorded, but if two crabs continuously engaged one another, only one fight was recorded. However, if two crabs engaged one another multiple times, but showed aggressive behavior towards another crab in between confrontations, multiple fights were recorded for the initial crab pair. All observations were taken during the same week within two hours of high tide.

Laboratory Observations

In order to determine differences in rates of fighting based on density, a laboratory fighting experiment was established. A total of 120 crabs, 60 male and 60 female, were collected from the low-density Temae site (site 5). This site was chosen since it had the largest population of crabs to collect from, and only one site was used in order to control for any differences between crabs from different sites. Egg-bearing females were returned to the site and not used in any part of the experiment.

Once the crabs were collected, they were separated and each one was kept in a small cup with sediment and seawater. The crabs were then numbered and placed into three groups. Group 1 consisted of male crabs numbering 1-40, group 2 was female crabs numbering 1-40, and group 3 was a combination of male crabs 41-60 and female crabs 41-60. Crabs within each group were then placed into random pairs, 20 per group, making sure that all of the pairs in group 3 were male-female pairings. The groups were divided one last time into a small treatment and a large treatment with the first 10 pairs per group in the small treatment and pairs 11-20 in the large treatment. The two treatments were created to mimic high and low densities.

After the crabs were paired, sorted, and left to rest for 24 hours, experiments began. Each pair of crabs was placed into a rectangular enclosure and observed for 5 minutes. In order to prevent disturbance of the crabs, observations were made at a distance and the observation area was placed at the eye level of the observer. In addition, the observer made sure not to move at all during the observation period. Over the course of the 5-minute observation, a stopwatch was used to record the amount of time the crabs spent interacting aggressively. The definition of an aggressive interaction was the same as that used in the field portion of the study. Small treatment pairs were placed in a 10 cm by 15 cm arena, while large treatment pairs were placed in a 16 cm by 26 cm arena. All observations were done within three days of capture, and then the crabs were returned to their original habitat.

Statistical Analysis

All statistical tests were performed using JMP software. Both density and nearest neighbor data were independently analyzed using a one-way ANOVA to determine if the 8 study sites had significantly different amounts of burrows or significantly different distances between burrows. This analysis was followed by a Tukey-Kramer HSD test (one on each data set) to determine which sites, if any, were significantly different from one another. Salinity data were grouped by habitat type (mangrove/mudflat vs. stream/ditch) and then a T-test was run to see if there was any notable difference in salinity between the two groups. Finally, several T-tests and a two-way ANOVA were run on both the field and laboratory observations. One T-test was run on each gender pairing to assess the significance of differences in aggression between high and low density conditions. The two-way ANOVA was then used to determine whether there was any interaction between density and sex pairing. It was also used to find the significance of any differences between the two variables. Field and laboratory data were analyzed separately, but used the same types of statistical tests.

RESULTS

Habitat Comparison

The density of crabs, as represented by the average number of burrows, appeared to indicate four higher density and four lower density sites (Fig. 3). A one-way ANOVA confirmed that the sites were significantly different from one another ($F = 4.4$, $p = 0.002$). However, a Tukey-Kramer HSD test failed to find sites 1-4, the apparent "high" density sites, significantly different from sites 5-8, the "low" density sites. Only one site, site 2, had a significantly higher density when compared to sites 5-8, however the test did show that density at sites 5-8 did not differ significantly.

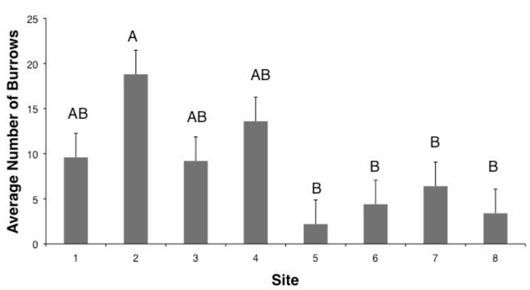

Fig. 3. Average number of burrows within a .25 m^2 area. Error bars represent +1 SE. A one- way analysis of variance followed by a Tukey-Kramer HSD test showed significantly higher density at site 2 when compared to sites 5-8. Bars that display the same letter above indicate densities that do not differ significantly.

The nearest neighbor data reflected the density results at all sites. As expected, sites with high density had low nearest neighbor measurements, and vice versa (Fig. 4). An ANOVA showed that the sites were significantly different from one another ($F = 4.6$, $p = 0.001$), but the Tukey-Kramer HSD test failed to completely distingish sites 1-4 from sites 5-8. The test did, however, show that sites 1, 2, and 4 were all significantly different from sites 5 and 8.

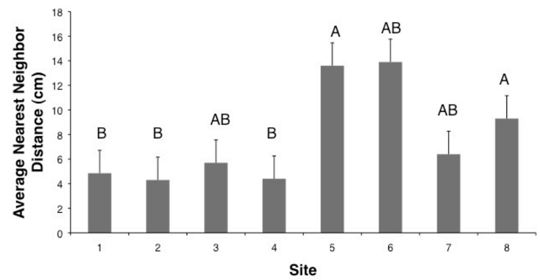

Fig. 4. Average nearest neighbor distance between burrows at each site. Error bars represent +1 SE. A one-way analysis of variance followed by a Tukey-Kramer HSD test showed significantly lower nearest neighbor distance at sites 1, 2, and 4 when compared to sites 5 and 8. Bars that display the same letter above indicate nearest neighbor distances that do not differ significantly.

Differences across sites in salinity, the final habitat comparison, were consistent with the density and nearest neighbor data, showing differences between sites 1-4 and sites 5-8, the former with lower salinity, and the later with higher salinity (Table 1). Since each site only had one salinity measurement, the four low salinity sites were considered as one group, and the four high salinity sites were considered another. When tested, the

Table 1. Salinity data in parts per thousand (ppt) for each of the 8 field sites.

Site	Salinity (ppt)
1	3
2	15
3	2
4	10
5	23
6	32
7	35
8	36

two groups were found to have significantly different salinity levels (T-test, $t = 5.63$, $p = 0.001$)

Field Observations

Using three separate T-tests, it was discovered that male-male, male-female, and female-female gender pairings all had a significantly higher number of aggressive interactions at the high-density site when compared to the low-density site (Fig. 6; Table 2).

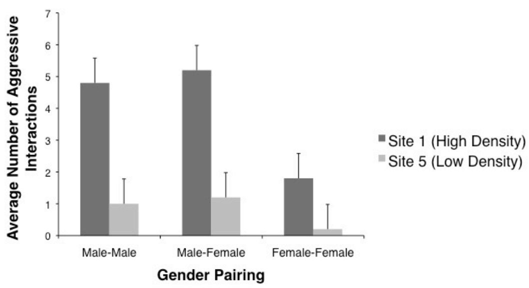

Fig. 6. Average number of male-male, male-female, and female-female aggressive interactions at one high-density and one low-density site. Error bars represent +1 SE. The effects of both density and sex pairing were significant (see text, Table 3). The high-density sites also had a significantly higher amount of aggressive interactions for each sex pairing (see text, Table 2).

After running the T-tests, a two-way ANOVA was used to understand the effects of density and type of sex pairing on the number of aggressive interactions. The results showed that density and sex pairing are each important in determining the number of aggressive interactions between crabs. However, there was not an interaction between density and sex pairing, meaning that the difference between the number of aggressive interactions at high and low densities does not differ markedly when the sex pairings are compared to one another (Table 3; Fig. 6).

Laboratory Observations

As with the field observations, a T-test was run for each gender pairing to examine the differences between the amount of time crabs spent engaged in aggressive interactions

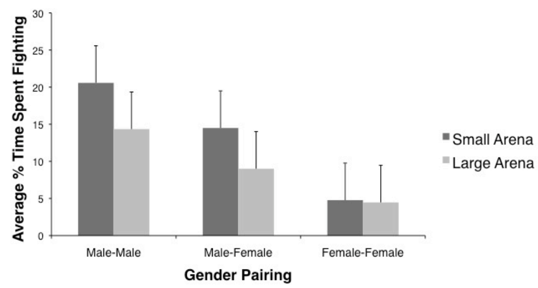

Fig. 7. Comparison of the average percent of total observation time each gender pairing spent engaged in aggressive interactions when placed in a small arena versus a large arena. Error bars represent +1 SE. The effects of sex pairing were significant (see text, Table 7). There was not a significant difference between the time spent fighting in the small versus large arenas (see text, Table 2).

Table 2. Results of the T-tests run on each of the sex-pairs comparing aggressive interactions at high and low density. All three pairs were found to exhibit significantly more aggressive interactions at the high-density site. Stars represent significant p values.

Sex Pairing	**DF**	**T Value**	**P Value**
MM	8	2.81	0.013*
MF	8	3.55	0.0068**
FF	8	5.37	0.0009***

Table 3. Results of a two-way ANOVA analyzing the effects of density and sex pairing on the number of observed aggressive interactions between crabs. Both density and sex pairing were significant. Stars represent significant p values.

Source	**DF**	**F Value**	**P Value**
Density	1	32.04	<0.0001***
Sex Pairing	2	4.38	0.02*
Density-Sex Pairing Interaction	2	1.42	0.26

in a small arena (which represents high density) versus a large arena (which represents low density). The tests showed that, under laboratory conditions, there was no significant difference between the amount of time spent fighting in the small arena versus the amount of time spent fighting in the large arena. This was true for male-male, male-female, and female-female pairs (Fig. 7; Table 4).

Though the results of the three T-tests were not significant, a two-way ANOVA was run on the laboratory data as well. Much like the field data, no interaction was found between arena size and sex pairing. The test did show that sex pairing is an important factor in determining the amount of time crabs spend engaged in aggressive interactions, but in this case density (represented by arena size) did not play an important role in the amount of time crabs spent fighting (Table 5; Fig. 7).

DISCUSSION

Habitat Comparison

Each of the habitat comparison measurements showed trends that support the grouping of sites 1-4 and sites 5-8. Though Tukey-Kramer results for density and nearest neighbor did not find significant differences between all of the sites in the first group and all of the sites in the second group, no significant differences were found within a group, and general groupings of the highest values and lowest values for each set of measurements always lined up with the 1-4 and 5-8 site division (Fig 3; Fig 4). Lack of significance could have been due to the limited number of quadrats measured at each site.

In addition, salinity measurements displayed significantly higher salinity at sites 5-8 when compared to sites 1-4 (Table 1). Even though the density and nearest neighbor data did not show significant differences between the first and second group of sites as a whole, the data is, arguably, enough to deem sites 1-4 and sites 5-8 different types of sites, especially when combined with the salinity data. In some species of fiddler crabs, a negative correlation between salinity and abundance has been observed (Miller and Maurer 1973). Using this information, sites 1-4 were considered "high" density sites and sites 5-8 were considered "low" density sites. These two site classifications were needed to further test the finding that density dependent processes such as competition increase at higher densities (Raven and Johnson 1989).

Field Observations

Field observations revealed that both male and female crabs engage in significantly more aggressive acts in a high-density population when compared to a low-density population (Table 2). This finding supports my hypothesis that competition between crabs would increase at higher densities for all gender pairings. Field results also showed that both density and gender pairing have a significant impact on the amount of aggressive interactions between crabs. These results further support the fact that higher density populations yield more competition. In addition, the significant effect of gender pairing on aggressive interactions could be

Table 4. Results of the T-tests run on each of the sex-pairs comparing time spent engaged in aggressive interactions in the large and small arenas. None of the sex pairings showed a significant difference in time spent fighting in the small or large arenas.

Sex Pairing	DF	T Value	P Value
MM	18	0.84	0.21
MF	18	0.74	0.23
FF	18	0.06	0.48

Table 5. Results of a two-way ANOVA analyzing the effects of arena size and sex pairing on the percentage of time crabs spent engaged in aggressive interactions. Sex pairing was significant. The star represents a significant p value.

Source	DF	F Value	P Value
Arena Size	1	1.08	0.30
Sex Pairing	2	3.70	0.03*
Arena Size-Sex Pairing Interaction	2	0.23	0.79

one reason why so little is known about aggression in female fiddler crabs. Males may simply be involved in more fights. From this data, it is clear that the expected increase in competition in higher density populations holds true for all sex pairings of the fiddler crab, *U. crassipes*. However, the same results could not be replicated in the laboratory.

Laboratory Observations

Unlike observations made in the field, laboratory tests failed to show a significantly greater amount of aggressive interaction in the high-density condition (Table 4). Even though the T-tests did not find a significant difference between the two laboratory conditions, the crabs in all three sex pairings spent more time fighting in the small arena (high-density) than in the large arena (low-density). It is possible that the lack of significance is due to the forced interactions created in a laboratory setting, and reduced aggression could have been caused by the stress of captivity. Since aggression in fiddler crabs is most often linked to defense of territory, the lack of burrows and a personal territory in this arena-style fighting experiment may have also resulted in a decrease in aggression between crabs (Hyatt and Salmon 1978). That being said, the laboratory observations were able to confirm the field observation that sex pairing significantly impacted the amount of time crabs spent fighting. This further demonstrates that, regardless of the population density, gender is an important factor in determining how much time a fiddler crab spends fighting.

Limitations and Recommendations

The habitat, field, and laboratory findings presented here have opened the door to many more questions about the habitat requirements and behavior of *Uca crassipes* on Mo'orea. Given more time and materials, one could better understand the differences between the traditional mudflat and mangrove habitats and the more unusual streamside and ditch habitats. Not only would it be beneficial to discover other environmental factors that differ between the two types of sites, but it would also be extremely useful to examine the relationship between the fiddler crab populations and the varying amount of human influence surrounding them. Perhaps the stream and ditch populations in Maharepa are actually remnants of larger mudflat populations that have been diminished by the large amount of human development in that area.

Further behavioral studies could also be done to explore how factors other than density impact aggression in fiddler crabs on Mo'orea. Since shore level, sediment size, temperature, organic matter content, and salinity are all thought to be important factors in burrow selection, it is possible that they also play a role in the territorial nature of fiddler crabs (Koch et al. 2005). In this study, significantly higher salinity levels corresponded with lower density, so perhaps salinity is another factor, in addition to density, that causes differences in aggressive interactions in *U. crassipes*.

Finally, improved laboratory conditions, as stated previously, would shed more light on the exact relationship between population density and fighting in *U. crassipes*. Males in other fiddler crab species have been seen defending territories as small as 7-10 cm in diameter, meaning that the "small" arena in my laboratory experiment may have still been too big to result in a significant difference in fighting due to density (Zucker 1974). Additionally, it would be interesting to see if the fiddler crabs behave differently in conditions where they are allowed to establish burrows or territories when compared to a condition such as the one used in this study where neither crab has a pre-established territory.

Conclusions

This study has shown that, in the field, aggression increases with density in male-male, male-female, and female-female pairs of the fiddler crab *Uca crassipes*, as predicted by existing knowledge of density dependent processes. It has also illuminated the difficulty of replicating such results outside of a natural setting. The implications of these findings are two-fold. Primarily, they support the idea that density dependent processes, such as competition, increase as population density increases. Secondly, they remind all scientists that observations of an animal's behavior in nature are generally more accurate than those seen in the artificial conditions created in a laboratory experiment. Laboratory tests are important in isolating specific variables that are believed to engender a particular behavioral response, but an awareness of an animal's environment as a whole is crucial in fully understanding any animal behavior.

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LITERATURE CITED

Bihler, A. 2005. Habitat selection and spatial distribution of two fiddler crab species (*Uca crassipes* and *Uca tetragonon*). Pp, 13-19 in Biology and Geomorphology of Tropical Islands: Student Papers 2005. University of California, Berkeley.

Crane, J. 1975. Fiddler Crabs of the World. Princeton University Press, Princeton, New Jersey.

deRivera, C. E., Backwell, P. R. Y., Christy, J. H., Vehrencamp, S. L. 2003. Density affects female and male mate searching in the fiddler crab, *Uca beebei*. Behav Ecol Sociobiol 53:72-83.

How, M. J., Hemmi, J. M., Zeil, J., Peters, R. 2007. Claw waving display changes with receiver distance in fiddler crabs, *Uca perplexa*. Animal Behaviour 75(3):1015-1022.

Hyatt, G. W., Salmon, M. 1978. Combat in the Fiddler Crabs Uca pugilator and U. pugnax: A Quantitative Analysis. Behaviour 65 (3/4):182-211.

Koch, V., Wolff, M., Diele, K. 2005. Comparative population dynamics of four fiddler crabs (Ocypodidae, genus *Uca*) from a North Brazilian mangrove ecosystem. Marine Ecology Progress Series 291:177-188.

Miller, K. G., Maurer, D. 1973. Distribution of the Fiddler Crabs, *Uca pugnax* and *Uca minax*, in Relation to Salinity in Delaware Rivers. College of Marine Studies Contribution 83: 219-221.

Nicholson, A. J. 1954. An outline of the dynamics of animal populations. Australian Journal of Zoology 2(1):9-65.

Raven, P.H., Johnson, G. B. 1989. Biology. Times Mirror/Mosby College Publishing:446-460.

Yamaguchi, T., Tabata, S. 2005. Territory usage and defense of the fiddler crab, *Uca lacteal* (De Haan) (Decapoda, Brachyura, Ocypodidae). Crustaceana 77(9):1055-1080.

Zucker, N. 1974. Shelter building as a means of reducing territory size in the fiddler crab, *Uca terpsichores* (Crustacea: Ocypodidae). American Midland Naturalist 91(1):224-236.