

PARASITE ABUNDANCE AND COLOR-BIASED PREDATION OF FIDDLER CRABS, *UCA CRASSIPES*, IN MOOREA, FRENCH POLYNESIA

LISA GUAN

Environmental Science Policy and Management, University of California, Berkeley, California 94720 USA

Abstract. This study investigates parasite abundance and differential predation vulnerabilities of the fiddler crab *Uca crassipes* in Moorea, French Polynesia to explore parasite transmission strategies. Fiddler crab dissections measured parasite count and examined differences in parasite load among several crab characteristics: sex, size, color, and habitat. Crabs with larger carapaces and claws had greater parasites loads. Predation experiments were conducted to assess avian predatory preferences of the fiddler crabs based on phenotypic characteristics. Experimental results revealed that avian predators preferred to prey on crabs with claws of lower degrees of redness, regardless of crab size. No correlation was found between parasite abundance and predatory preferences. Crab morphologies may serve as indicators of vulnerabilities to parasitic infection and avian predation.

Key words: *fiddler crabs; Uca; parasites; trophic transmission; predation; color; sexual dimorphism*

INTRODUCTION

Parasitism can be broadly defined as a close relationship in which an organism feeds dependently on a living host without death to the host (Gunn and Pitt 2012). Nearly 50% of animal species can be classified as parasites and almost 20% of all animal species are parasites that directly live in or on their hosts for most of their lives (Poulin and Morand 2000). Parasites rely heavily on hosts for habitat and dispersal. They often transfer from one host to another through trophic strategies (Lafferty and Kuris 2002). Many parasites infect several intermediate hosts—organisms that are preyed upon by subsequent hosts—before reaching a final host. Most cestodes, nematodes, trematodes, and all acanthocephalans depend on a final, definitive host consuming an intermediate host, i.e. trophic transmission, a strategy that allows them to survive predation of one host by another (Lafferty 1999). Trematodes, typically infect three hosts in succession throughout their life cycle by means of trophic transmission—the first host is usually a mollusk or gastropod, the second a crustacean, and the third a vertebrate (Combes 2002 and Sousa 1993). The dependency of some parasites on trophic transmissions suggests that it would be beneficial for the parasite to select intermediate hosts that are vulnerable to predatory subsequent hosts.

To optimize parasite life cycle progression, parasites have been known to alter host phenotypes (Miura 2006). A study on a parasitic nematode in the ant species *Cephalotes atratus* demonstrated that infection by parasites manipulated ant abdomens to resemble red berries, making them more likely to be eaten by birds (Lefevre 2008). Studies have also shown that trematode infection in snails causes gigantism and forces them to occupy a different ecological niche (Miura 2006). By causing snails to exploit a new habitat otherwise not used by snail populations, parasites expose themselves to an area with greater probabilities of developmental success.

Fiddler crabs (*Uca spp.*) have been observed to be second intermediate hosts for trematodes (Smith et al. 2007). Some hosts are infected more frequently than others due to more exposure to the free-living, infective stages of the trematodes (Adamson 1994). This suggests that there can be differences in parasite prevalence within one population of hosts depending on degree of exposure to infective stages of trematodes. Free-living stages of trematodes do not actively search and pursue their hosts; rather, they search for the space and time where they have the highest probability of meeting their hosts (Combes 2002). It is in the trematode's best interest to infect a host that will be likely consumed by the next successional host.

Fiddler crabs display a high degree of sexual dimorphism. Males have one large, red claw while females have two claws of equal size. This male display of fighting ability and attractiveness to mates comes at the expense of reduced survival (Darwin 1871). Male fiddler crabs with their large claws and brighter colors are more conspicuous than cryptic females (Koga 2001). Their large claw may prevent rapid escape from predators, such as birds. These sexually selected traits may increase predation of male fiddler crabs (Koga 2001).

On Moorea, *Uca crassipes* is an abundant fiddler crab species found in several mangrove habitats. To date, no studies have been done on parasites in *U. crassipes* and no studies have investigated the predation of these particular fiddler crabs. This study investigated parasite prevalence and predation rates in *U. crassipes* in terms of sex, carapace size, claw size, habitat, and color. The goal of the study was to explore the role of selection in trematode transmission strategies by examining correlations between parasite prevalence and predation preference by final hosts.

METHODS

Study site

Data were collected on the island of Moorea, French Polynesia during October and November 2013. *Uca crassipes*, the thick-legged fiddler crab, is a relatively small species, between 7-21mm in length, and abundant in mangrove habitats. Field surveys were conducted at three sites (Fig. 1) on the western side of Moorea. All three sites had populations of *U. crassipes*, but varied in their substrate composition and degree of tidal influence. The sites represented different intertidal mangrove habitats with different population densities of *Uca crassipes*. Site 1 is a mangrove habitat with sandy substrate approximately two kilometers north of Ha'apiti. Site 1 is highly influenced by tidal fluctuations with most of the beach submerged during the high tide. Site 2 is approximately one kilometer north of Ha'apiti. Mangroves are present on the northern edge of the site but it is dominated by grass and mud substrate and is not largely influenced by the tides. Site 3 is on the northern coast of Mo'orea. Site 3 consists of a younger mangrove stand with

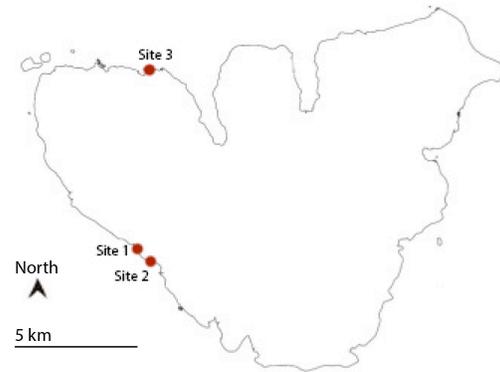


FIG. 1. Study sites on Moorea, French Polynesia. Site 1: 2 km north of Haapiti (17°33'10.33"S, 149°52'49.69"W). Site 2: 1 km north of Haapiti (17°33'17.32"S, 149°52'44.39"W). Site 3: North shore of Moorea (17°29'30.74"S, 149°53'23.99"W). Map courtesy of UC Berkeley GIF.

coarse sandy substrate. It is also highly influenced by tidal patterns. *Uca crassipes* creates burrows in the sand or mud. Crabs were randomly collected by digging them out of their burrows with a shovel; this technique may be biased to capture the most visible crabs or the slowest ones. Population density was measured by randomly placing a 0.5x0.5 meter quadrat around the sites, counting the number of burrows within the quadrat, and averaging counts. An ANOVA analysis was performed to test for differences in crab population densities across the different sites. All data were analyzed using the statistical program R (R Development Core Team 2013).

Parasite abundance

Uca crassipes were collected from all three sites and transported alive to the UC Berkeley Gump station, where dissections were conducted to survey parasite prevalence. Crabs from each site were housed individually to avoid aggression between individuals. Cups were covered by mesh, contained mud and seawater, and kept at the UC Berkeley Gump station wet lab. Pictures of crabs were taken with Nikon CoolPix AW110 with a white standard. Data on sex, carapace size, and claw size were collected prior to dissection. A Wilcoxon rank sums test was used to determine differences in carapace size between males and females.

Initially, several organs, such as muscle tissue, hepatopancreas, stomach, and gills

were isolated and checked for parasites, but only the gills consistently yielded parasites. Gills from each crab were removed and mounted on microscope slides. Consequently, data from the gills are presented here. Trematode eggs (Appendix A) were found in gill tissue and were counted under a compound microscope at 200x magnification (Leica DM2500). A Wilcoxon Rank sums test was performed to test for differences in parasite load between males and females. A linear regression was used to investigate the relationship between carapace size and claw size in males. An ANOVA analysis was used to analyze differences in average parasite abundance among the three mangrove sites. The redness and brightness of fiddler crab claw color was quantified with Adobe Photoshop by first, adjusting photos of the crab to the white standard and then, recording the red color value from RGB values. A multiple regression was used to analyze relationships between parasite load and each of the following parameters: carapace size, claw size, and claw redness.

Voucher specimens of *Uca crassipes* and *U. crassipes* gills were deposited at the UC Museum of Paleontology.

Predation experiment

Field experiments on preference of fiddler crabs by bird predators were conducted at two mangrove sites – Sites 1 and 2. *U. crassipes* were collected using the same technique described above (i.e., shovel). Data on sex, carapace size, claw size, and claw color were collected. Crabs were glued down with Superglue to fishing line and individually tied to wooden dowels to be exposed to potential bird predators. The primary bird predators were mynas, although egrets, terns, and red-vented bulbuls were also observed in the area. The dowels were placed in the center of cardboard sheets to prevent crabs from burrowing into the substrate. The cardboard was covered with mud or sand to provide camouflage with the substrate. Crabs were randomly placed at each site approximately 1-2 meters away from one another. They were left for 1-2 hours and the ones that were eaten were recorded.

A Pearson's chi-squared test was performed to test for differences in predation rates between males and females. A chi-squared test was also used to test for differences in predation rates between Site 1 and Site 2. Color analyses on the redness and

brightness of claw color from photos of individual crabs were collected using Adobe Photoshop, as described above. A logistic regression using the generalized linear model was used to test the effect of carapace size and claw size on predation. A linear regression showed a relationship between claw size and claw color. Following that result, an ANOVA analysis was utilized to analyze relationships between predation rates and claw size with claw redness.

RESULTS

Parasite abundance

Parasite surveys in *Uca crassipes* tested the relationships between parasite abundance and sex, site, carapace size, claw size, and claw color. A total of 85 fiddler crabs were dissected. 71 crabs yielded trematode eggs (approximately 0.25 mm) in gill tissue and all parasites were counted. Parasite count in crabs ranged from 0 to over 600 and there was a significant effect of carapace size and claw size on parasite load. A multiple regression analysis, taking into account interactions between carapace size, claw size, and claw color, showed that carapace size and claw size significantly predicted parasite abundance [$R^2 = 0.13$, $F(7,49) = 1.08$, $P = 0.04$]. Parasite abundance increases as carapace size and claw size increases (Fig. 2). The interacting factors of carapace size and claw size have a highly significant positive correlation ($R^2 = 0.77$, $P < 0.001$).

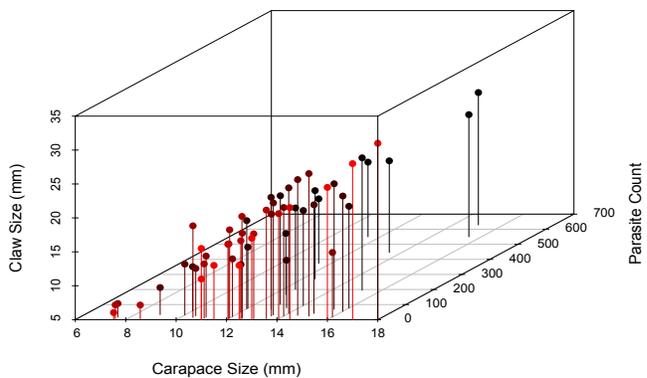


FIG. 2. 3D scatterplot showing parasite count with respect to claw size and carapace size (N=57). Parasite count is significantly correlated with claw size and carapace size.

57 male crabs and 28 female crabs were collected for dissection. Although males ($\bar{x} = 12.7$ mm, $SD = 2.3$) have significantly larger

carapace ($W = 462, P = 0.002$) than females ($\bar{x} = 11.1$ mm, $SD = 1.9$), there was no significant difference in total number of parasites per crab between males and females (Fig. 3; $W=580, P = 0.53$).

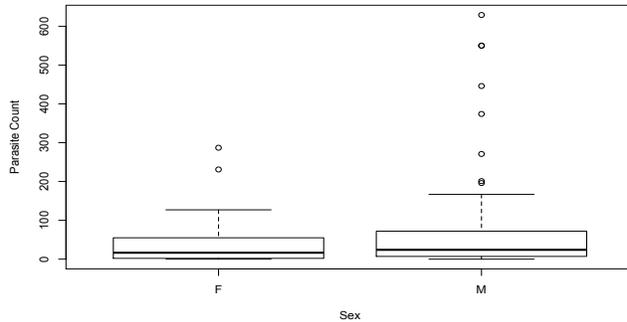


FIG. 3. Effect of sex on parasite abundance (N=85). No significant difference in parasite count between males and females.

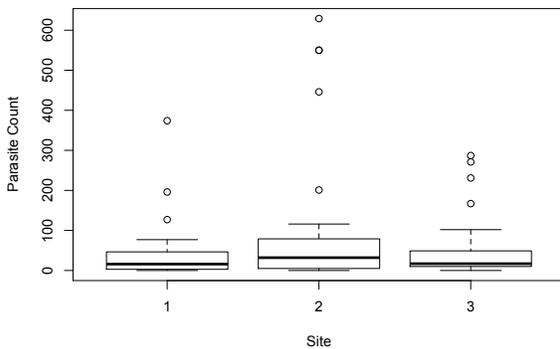
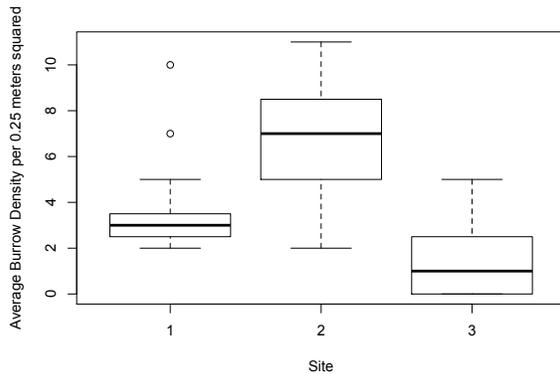


FIG. 4. ABOVE Effect of site on crab burrow density (N=85). There was a significant difference in site density among the three sites.

FIG. 5. BELOW Effect of site on parasite count (N=85). There is no significant difference in parasite count among the sites.

There was a significant difference between average burrow densities at each site [Fig. 4; $F(1,43) = 4.038, P = 0.05$], but there was no significant difference in total number of

parasites per crab between Sites 1, 2, and 3 [Fig. 5; $F(1,83) = 0.16, P = 0.70$]. This suggests that crab population density has no effect on parasite abundance.

Predation experiment

Predation experiments at Sites 1 and 2 tested whether there is a relationship between predation by birds and site, sex, carapace size, claw size, and claw color. There was no significant difference in predation of crabs between Site 1 and Site 2 ($\chi^2 = 0.42, df = 1, P = 0.52$). 52 male fiddler crabs and 30 females were exposed to predation by birds. A greater proportion of females were eaten compared to males, but this difference was not significant (Fig. 5; $\chi^2 = 0.52, df = 1, P = 0.47$). Carapace size was not correlated with predation [GLM(poisson), $\chi^2 = 1.4, P = 0.24$]. Claw size was not correlated with predation [GLM(poisson), $\chi^2 = 2.8, P = 0.09$].

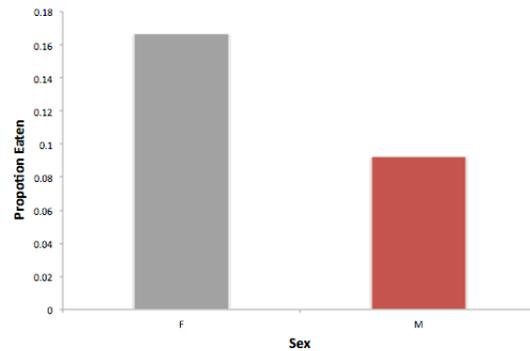


FIG. 6. Effect of sex on predation rates (N = 82). Male = 0.108; Female = 0.167. There was no significant effect of sex on avian predator preference.

A linear regression showed a strong significant positive correlation between claw size and claw color (Fig. 7; $R^2 = 0.33, P < 0.001$). Due to this interaction, an ANOVA analysis was used to test whether there was a relationship between claw redness and claw size with predation. The ANOVA accounted for the significant interaction between claw size and claw redness, and yielded the following result: when claw size was controlled, claw redness was significantly negatively correlated with predation [$F(1,35) = 6.5, P = 0.015$]. Crabs with claws of a lower degree of redness were more likely to be predated on, regardless of claw size (Fig. 7).

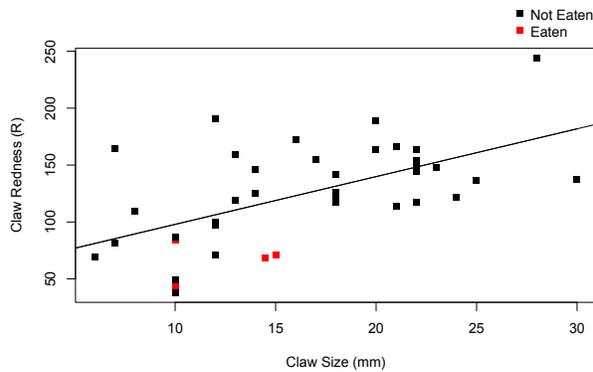


FIG. 7. Effect of claw redness and claw size on male predation (N = 52). Claw redness and claw size are strongly correlated as shown through the regression line.

DISCUSSION

Parasite abundance

The parasites found in *Uca crassipes* gills were unidentified trematode eggs (Appendix A), a non-reproductive life stage of trematodes. This suggests that the infective parasites' main purpose is to be passed onto the subsequent host so that it will be able to develop into the next life stage (Lafferty 1999). Typically, trematode eggs are free-living and will infect a primary intermediate host, usually a gastropod, once it has hatched (Sousa 1993). No previous research has reported trematode eggs in crabs. This particular species of trematode may have a life cycle that is not yet known. An alternative explanation could be that parasites entered the crab accidentally. If this is an accidental infection, the crabs could serve as a dead-end host if the parasites fail to develop inside birds after trophic transmission.

Parasite abundance was found to increase with carapace size and claw size. Results coincided with expectations based on Muira's (2006) study that showed parasites might alter host phenotypes, increasing the likelihood of trophic transmission. All three parameters: parasite abundance, carapace size, and claw size were positively correlated with one another (Fig. 2). This positive correlation may be due to another variable: time—as crabs age, they grow in carapace size and claw size and may accumulate more parasites with time. Parasite abundance in *U. crassipes* did not vary among color, sex, site location, and population density. Despite a significant difference in carapace size with respect to sex,

there was no significant difference in parasite load between males and females. The male fiddler crab's ornamental claw does not function a tool for feeding, prolonging its foraging time (Johnson 2003), leading to the hypothesis that longer feeding time will create more exposure to parasites. The lack of a significant difference in parasite abundance between males and females indicates that accumulation of parasites may not be due to differences in foraging behavior. The presence of parasites is likely omniscient in the habitat, independent of feeding source, and equally accessible to males and females.

Crab population densities varied among the three sites but there was no significant difference in average parasite abundance. Parasite presence at a location may be influenced by final host presence or abundance (Lafferty 1999). The birds that preyed on the crabs may be the final host for the parasites. Sites that are within a habitat range may not show any differences in parasite load, in spite of distinct site characteristics, because bird habitats can span a large area of the island.

Further studies should investigate the presence of parasites in other organisms in the system, such as snails. A list of snails that have been dissected for parasite presence is included in Appendix A. Discovery of other life stages of the parasite can give insight to the life cycle and transmission of the trematode. Another fiddler crab species, *Uca tetragonon*, is also found on Moorea and was observed at Site 3. Comparison of parasite abundance in both species can provide more information on the preferred host characteristics of the parasite.

Predation experiment

Previous studies have shown that presence of a large claw decreases escape endurance (Allen 2007) and may increase likeliness of predation in males. Results revealed no significant difference in predation rates between males and females. In this system, a higher chance of predation is not a cost of bearing an ornamental weapon. Bildstein's (1989) study showed that large claws in males served as weapons that warded off avian predators. Contrary to what Bildstein demonstrated, experimental predation results showed that an enlarged claw does not serve as a defense mechanism since there was no preference between male and female crabs. This may be due to the

experimental design, in which the crabs were tied down and limited in their movement. It is possible that if given free range of motion, males would exhibit aggressive behavior that can fend off predators.

Field experiments showed that predation significantly varied with respect to claw color. Contrary to the expectation that males' brightly colored claws may increase male predation rates (Koga 2001), crabs with a lower degree of claw redness were more likely to be preyed upon by birds. When claw size was controlled, to account for the significant interaction between claw size and claw color, redness of the claw was still significantly negatively correlated with predation. Carapace size was also not correlated with predation rates. A possible explanation is that there are other red, harmful objects in the habitat that the birds have learned to avoid. A red claw may be associated with danger and used as a warning signal, regardless of the size of the crab.

Predation rates did not vary significantly with respect to location. Site 1 and Site 2 were relatively close to one another and fall within the same habitat range for birds. The lack of variation in predators could explain the insignificant difference in crab predation rates at the two sites.

Further studies can be done on the feeding preferences of birds aside from fiddler crabs. Many birds, such as mynas, were not strictly shorebirds and could have an extensive diet. More information on what they prefer to eat could provide evidence on why birds avoided bright red claws.

CONCLUSION

Parasite abundance in *Uca crassipes* cannot be explained, through proxy of sex, size, or color, by the likeliness of predation and trophic transmission. The presence of a previously undescribed parasite provides excellent opportunities to explore a novel parasitic life cycle. The male fiddler crab's costly ornamental claw has shown to benefit those with conspicuously bright claws by decreasing chances of predation. Fiddler crabs serve as a model for studying the consequences and advantages of sexual dimorphism.

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APPENDIX A



FIG. 8. Unidentified trematode egg photographed at 200x magnification under a Leica DM2500 compound microscope.

List of Dissected Snail Species
<i>Cerithium spp.</i>
<i>Gibberulus gibberulus</i>
<i>Littorina coccinea</i>
<i>Mitra mitra</i>
<i>Maculotriton serriale</i>
<i>Morula granulate</i>
<i>Morula striata</i>
<i>Nerita argus</i>
<i>Nerita plicata</i>
<i>Neritina canalis</i>
<i>Terebra sp.</i>
<i>Thiara granifera</i>
<i>Vexillum cadaverosum</i>

TABLE 1. List of snail species dissected for parasites. No infected snails were found from this list.