

THE TERRITORIAL AGONISTIC BEHAVIORS OF TWO ANEMONEFISH: *DASCYLLUS TRIMACULATUS* AND *AMPHIPRION CHRYSOPTERUS*

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Abstract. Heterospecific agonistic behavior is difficult to study because there is so much uncertainty between species, but it is still an important component to shaping the dynamics of the community. Two fish (*Dascyllus trimaculatus* and *Amphiprion chrysopterus*) are symbiotic with the anemone *Heteractis magnifica* in Mo'orea, French Polynesia and exhibit territoriality. By quantifying their territorial behaviors, the two species served as a comparative model to study heterospecific agonistic behaviors. I found that *A. chrysopterus* showed higher aggression frequencies towards neighbors and intruders, while *D. trimaculatus* showed higher percentages of attacking various fish species. Territory sizes varied greatly within each species and were not different between *A. chrysopterus* and *D. trimaculatus*, and *D. trimaculatus* population sizes had a relationship with anemone size while *A. chrysopterus* population sizes did not. This work exemplifies how the complexities of heterospecific relationships can be quantified and how these interactions are influential to reef communities and ecology.

Key words: *anemonefish*; *Dascyllus trimaculatus*; *Amphiprion chrysopterus*; *territoriality*; *heterospecific aggression*; *agonistic behavior*; *Mo'orea, French Polynesia*

INTRODUCTION

A large amount of research on symbiosis, or heterospecific interaction, revolves around mutualism, in which both species benefit from the relationship (Vandermeer and Boucher 1978). Mutualisms are common and greatly contribute to biodiversity, and are important to study in an ecological context as well as an evolutionary context. Two types of mutualisms exist: obligate, in which one species depends on the other for survival, and facultative, where each species can survive without the other (Vandermeer and Boucher 1978). Another heterospecific interaction that receives less attention is heterospecific aggression – because there is a larger overlap in resources between conspecifics, conspecific aggression is usually more apparent leaving heterospecific aggression overlooked. Nonetheless, heterospecific aggression is very prevalent since species competing for the

same resources share similar methods to obtain and defend the resources, and the uncertainty in intent and communication between species induces a wide variation in heterospecific aggression (Peiman et al. 2010). It is important to consider this aspect of heterospecific interaction to fully understand community structure and dynamics in ecology, and little has been done to investigate differences in territorial behavior in similar systems.

In Mo'orea, French Polynesia, the anemone *Heteractis magnifica* plays host to two species of fish: *Dascyllus trimaculatus* and *Amphiprion chrysopterus*. The anemone is crucial in protecting the fish from predators; the fish hide in or around the anemone's tentacles as the stinging nematocysts of the anemone deter predators. In return, the fish protect the anemone from predation by attacking fish that prey on anemone tentacles such as chaetodontids (Holbrook and Schmitt

2005). Other benefits fish provide to the anemone are unclear, however Fautin (1991) hypothesized that the anemones could be obtaining nutrients from the fish's fecal matter, similar to how corals obtain nitrogen from fecal matter of large schools of grunts (Meyer and Schultz 1985). Another hypothesis is that the mutualistic protection allows the anemone to remain expanded for a longer period of time allowing the zooxanthellae more time to photosynthesize (Holbrook and Schmitt 2005).

Juvenile *Dascyllus trimaculatus*, known commonly as the three-spot damselfish, take refuge in and defend *H. magnifica*. *Dascyllus trimaculatus* often live in groups of varying numbers on the anemone; however, it is unknown if anemone-mates are related because the species exhibits a planktonic larval stage (Holbrook and Schmitt 2004). This damselfish feeds on plankton in the water column during the day and takes shelter in crevices at night (Holbrook and Schmitt 2005). It has been observed that *D. trimaculatus* does not nestle into the anemone's tentacles for protection, but only hides around the anemone's base. Although it is unknown whether *D. trimaculatus* undergoes an acclimating procedure to prevent being stung by nematocysts, the minimal contact with the tentacles suggests it does not. Within a year, *D. trimaculatus* sexually mature and leave the anemone to become free ranging reef fish (Holbrook and Schmitt 2004). In Mo'orea, it is very rare to see an unoccupied anemone – almost all are occupied by juvenile *D. trimaculatus* which are sometimes accompanied by the anemonefish *A. chrysopterus*.

Amphiprion chrysopterus, or the orange-fin anemonefish, is found on many anemone species, and is also found on *H. magnifica* in Mo'orea. Because each anemone is usually only large enough to host two anemonefish, *A. chrysopterus* has evolved to live alone or in monogamous pairs that defend the anemone from other settling anemonefish (Holbrook and Schmitt 2004, Krebs and Davies 1987). *A.*

chrysopterus lives on its host anemone for life, and sometimes defends multiple anemones clustered within two meters of each other (Holbrook and Schmitt 2005). The anemone is especially important for the anemonefish's reproduction: *A. chrysopterus* lays its eggs near the base of the host anemone for protection and are defended very aggressively; the male tends to the clutch which hatches into planktonic larvae (Dhaneesh et al. 2009, Mitchell 2003, Moyer 1986). *A. chrysopterus* is a diurnal planktivore that shelters in crevices at night (Holbrook and Schmitt 2005). The anemonefish acclimates itself to the anemone by frequently brushing itself on the tentacles of the anemone and collecting a mucous coating that contains the anemone's nematocysts. Through this, they achieve a "chemical camouflage" that prevents the anemone from detecting the fish and thus the nematocysts remain unfired upon contact (Fautin 1991). Holbrook and Schmitt's (2005) study showed that the presence of *A. chrysopterus* greatly increases anemone growth and reproductive success; those that hosted two anemonefish had the highest fission rates, while the anemones that did not host any fish had higher than expected mortality rates.

The anemonefish mutualism with *H. magnifica* indirectly benefits *D. trimaculatus* by creating more habitat area for the damselfish to occupy. The relationship between *A. chrysopterus* and *D. trimaculatus* is unique because the benefits of mutualism ameliorate the negative effects of competition for the same limited resource (Holbrook and Schmitt 2004). Anemonefish coexistence with damselfish on the same anemone is possible because the anemonefish are less able to chase out damselfish with increasing anemone size (Holbrook and Schmitt 2004). Territoriality of several species of damselfish has been studied by looking at aggression towards conspecifics and heterospecifics and the conditions of the defended territory (Shima 1992, Katzir 1981, Brawley et al. 1977). Similarly, the territorial behavior and mutualism between anemonefish species and various anemones

have also been thoroughly explored in the past (Moyer and Sawyers 1973, Porat and Chadwick-Furman 2004). However, the territoriality differences between damselfish living on anemones and anemonefish have not yet been studied.

Although both fish rely on the *H. magnifica* for refuge, their relationship with the anemone differ. Past studies have shown that *A. chrysopterus* provides substantial benefits to the anemone which is reflected in increased anemone growth rate and fission rate. This is consistent with *H. magnifica's* vital role as *A. chrysopterus's* lifelong refuge and safe haven for egg clutches and mate. In contrast, the benefits *D. trimaculatus* provide are not as obvious and have not been studied as thoroughly; it is thought that *D. trimaculatus* does not significantly enhance nutrition to the anemone (Holbrook and Schmitt 2005). Although juvenile *D. trimaculatus* also exhibit aggressive behavior to defend their anemone from predation, it lacks the drive of reproductive pressures. *A. chrysopterus* has been observed to be more aggressive than *D. trimaculatus* and behaves as the dominant mutualist. In addition, *D. trimaculatus* populations are much lower on anemones that host both species than anemones that only host *D. trimaculatus* (Holbrook and Schmitt 2005).

In this study, I aimed to explore how territorial behaviors influence community dynamics in a system. I examined the differences in agonistic behavior between *D. trimaculatus* and *A. chrysopterus* to determine whether living in similar systems and competing for the same resource produces similar territorial behaviors. Because *A. chrysopterus* is a lifelong mutualist to the anemone, I expected it to exhibit aggressive behavior correspondent to its higher investment in the anemone's health. I hypothesized that *A. chrysopterus* would have a higher aggression frequency, a larger territory size, and live on a larger anemone size than *D. trimaculatus*.

METHODS

Surveying was performed by snorkel, limiting observation to shallow anemones that could be observed from the surface (around three to four meters deep). Field sites included Gump Reef, Opunahou Public Beach, and Temae Public Beach where several specimens of *H. magnifica* that house both *A. chrysopterus* and *D. trimaculatus* exist. To avoid disturbing the fish by my presence, I allowed three minutes for them to habituate prior to collecting data, and observed from the furthest distance possible that still allowed me to clearly see the fish (typically three to four meters from the anemone). All observations were done during the day, and data was not collected if currents visibly affected behavior during which fish spent the majority of the time swimming to fight the current.

Territory size and fish counts

Territory sizes and fish counts were recorded for thirty anemones that had only *D. trimaculatus* or both *D. trimaculatus* and *A. chrysopterus*. The boundary of a fish territory was defined as the furthest distance fish patrolled from the anemone. I recorded two estimates of territory radii along the substrate and one estimate of territory height, then averaged the three radii and calculated the volume of territory space in cubic meters by assuming a hemispherical territory shape. Radii were estimated by observing how far fish wandered and noting reference points in the substrate, then later using a transect tape to measure the distance from the center of the anemone to the reference points. A fish count of both species inhabiting the anemones was conducted to determine whether there is a correlation between territory size and number of inhabitants. Territory size per individual fish was calculated so that the two species could be compared using the Rank Sum Test. Because the average *A. chrysopterus* is six times larger than the average juvenile *D. trimaculatus*, *A. chrysopterus* territory sizes per

individual were divided by six to adjust for differences in fish sizes.

Aggression towards neighbors and intruders

The frequency of aggression towards neighbors or intruders was observed over ten minutes for thirty anemones that had only *D. trimaculatus* or both *D. trimaculatus* and *A. chrysopterus*. An attack was defined as an acceleration towards a fish that usually resulted in a short chase. The number of attacks towards conspecifics or heterospecific neighbors of each species was recorded during the trial. The size of the attacker for *D. trimaculatus* was categorized as small (less than 2.5 cm in length) or large (more than 2.5 cm in length). The number of intruders that faced an attack by either *D. trimaculatus* or *A. chrysopterus* was also recorded. Attacker size was also noted for intruder attacks. The total number of fish that swam within one meter of the anemone was also recorded to adjust for differing fish densities. The number of attacks towards intruders was later divided by the number of fish that swam within one meter of the anemone to achieve an intruder attack proportion. Intruder attack proportions were compared among *A. chrysopterus* and large and small *D. trimaculatus*.

Aggression towards various fish species

Models of different reef fish were painted on pieces of plastic and attached to fishing line and a weight, and presented to twenty-nine *D. trimaculatus* and seven *A. chrysopterus* in their natural setting. The model fish species included *D. trimaculatus*, *A. chrysopterus*, *Chromus iomelas* (an herbivorous reef fish), and *Chaetodon lunula*, a fish that feeds on *H. magnifica*. While presenting the models to the fish, I recorded whether the fish took refuge, attacked, or had no reaction. I took caution to

swim very slowly with the model to the anemone, and avoided diving down towards the anemone by reeling out enough fishing line for the model to reach the depth of the anemone. I allowed ten seconds for the fish to notice and react to the model.

RESULTS

Territory size and fish counts

The defended territory size of *A. chrysopterus* did not differ from that of *D. trimaculatus* (Fig. 1). *A. chrysopterus* patrolled an adjusted average territory size of 0.277 m³ per fish, while *D. trimaculatus* patrolled an adjusted average territory size of 0.421 m³ per fish. However, territory sizes within both species was not normally distributed, and a Wilcoxon Rank Sums test showed that the overall differences in average adjusted territory sizes were not statistically significant ($Z=0.897$, $P=0.37$).

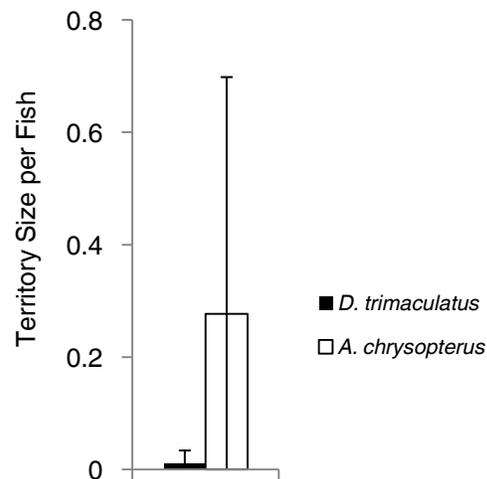


FIG. 1. Average adjusted territory size per fish for *D. trimaculatus* (0.421 m³) and *A. chrysopterus* (0.277 m³) were not statistically different. (Wilcoxon Rank Sums test, $Z=0.897$, $P=0.37$)

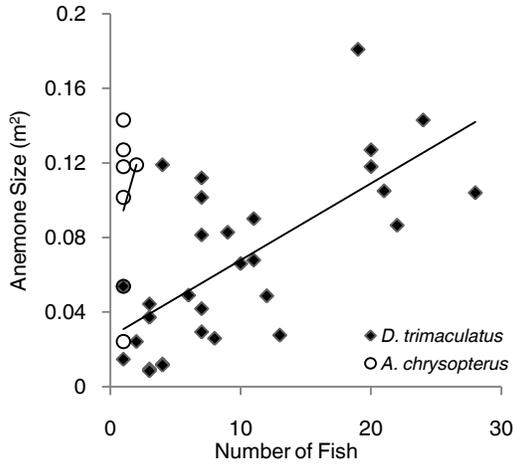


FIG. 2. Linear regressions of the number of fish versus anemone size. *D. trimaculatus* showed a significant trend ($F=25.1$, $d.f.=29$, $R^2=0.473$, $P<0.0001$), while *A. chrysopterus* did not show a significant trend ($F=0.24$, $d.f.=6$, $R^2=0.173$, $P=0.644$).

A linear regression in Fig. 2 showed there was a relationship between anemone size and number *D. trimaculatus* present ($F=25.1$, $d.f.=29$, $R^2=0.473$, $P<0.0001$), while there was no apparent relationship between anemone size and number of *A. chrysopterus* ($F=0.24$, $d.f.=6$, $R^2=0.173$, $P=0.644$). Past studies have shown that the presence of *A. chrysopterus* greatly affects anemone size and growth, but I did not have enough replicates to obtain clear results (Holbrook and Schmitt 2005).

Aggression towards neighbors and intruders

The frequency of attacks towards neighbors and conspecifics differed between *D. trimaculatus* and *A. chrysopterus* (Fig. 3). During the ten minute trials, Small *D. trimaculatus* attacked conspecifics on an average of 1.32 times while large *D. trimaculatus* attacked conspecifics on an average of 2.45 times. *D. trimaculatus* was never observed attacking *A. chrysopterus*, so its conspecific attack frequencies were identical to its neighbor attack frequencies. Although *A. chrysopterus* did not attack conspecifics, it attacked *D. trimaculatus* neighbors on an

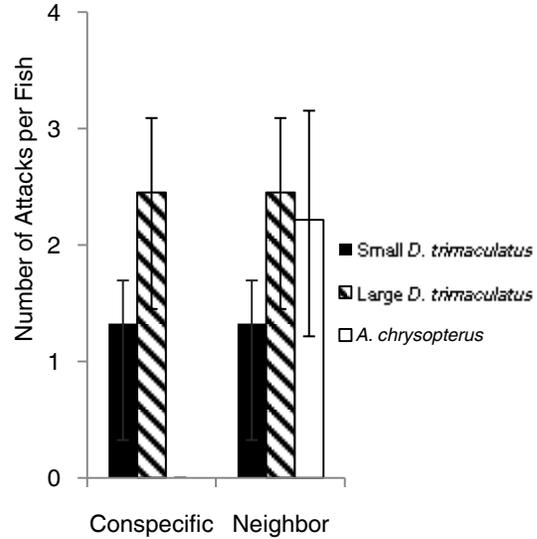


FIG. 3. Average number of attacks per fish towards conspecifics and neighbors for small *D. trimaculatus*, large *D. trimaculatus*, and *A. chrysopterus*.

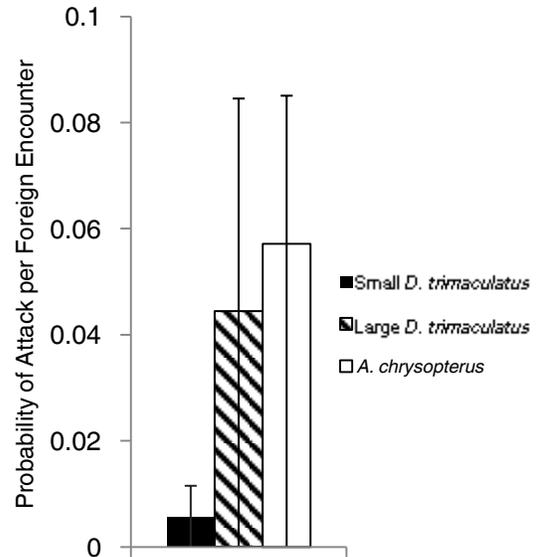


FIG. 4. Intruder attack proportions for small *D. trimaculatus*, large *D. trimaculatus*, and *A. chrysopterus* are significantly different (Kruskal-Wallis one way ANOVA, $H=9.307$, $d.f.=2$, $P=0.01$).

average of 2.21 times during the ten minute trials.

The intruder attack proportions varied among small *D. trimaculatus*, large *D. trimaculatus*, and *A. chrysopterus* (Fig. 4). *A.*

chrysopterus was the boldest, with an intruder attack proportion of 0.0571. Large *D. trimaculatus* followed with a proportion of 0.0444. Lastly, small *D. trimaculatus* was the least likely to attack with an intruder attack proportion of 0.00574. A Kruskal-Wallis one way ANOVA showed that the differences between the intruder attack proportions of each species were statistically significant ($H=9.307$, $d.f.=2$, $P=0.01$).

Aggression towards various fish species

The differences in behaviors towards different fish models were only drastically different for the *D. trimaculatus* model (Fig. 5a). *D. trimaculatus* usually did not respond to the extra neighbor, showing no reaction to the *D. trimaculatus* model 92.9% of the time, attacking 3.57% of the time and taking refuge 3.57% of the time. On the contrary, *A. chrysopterus* showed no reaction 30% of the time, but took refuge 50% of the time and attacked 20% of the time.

The slight difference in behaviors towards the *C. lunula* model shown in Fig. 5b was interesting. Both fish tended to take refuge with a probability of 82% for *D. trimaculatus* and a probability of 100% for *A. chrysopterus*. However, a few *D. trimaculatus* dared to attack (14%) or showed no reaction (4%), while *A. chrysopterus* never attacked or showed no reaction to the model.

Behaviors towards the *A. chrysopterus* model (Fig. 5c) were similar for each species (*D. trimaculatus*: Refuge=79%, Attack=0%, No reaction=21%, *A. chrysopterus*: Refuge=70%, Attack=0%, No reaction=30%). Behaviors towards the *C. iomelas* model (Fig. 5d) were also similar between each species (*D. trimaculatus*: Refuge=29%, Attack=0%, No reaction=71%, *A. chrysopterus*: Refuge=40%, Attack=0%, No reaction=60%).

DISCUSSION

The results of my research indicate a difference in some aspects of territorial

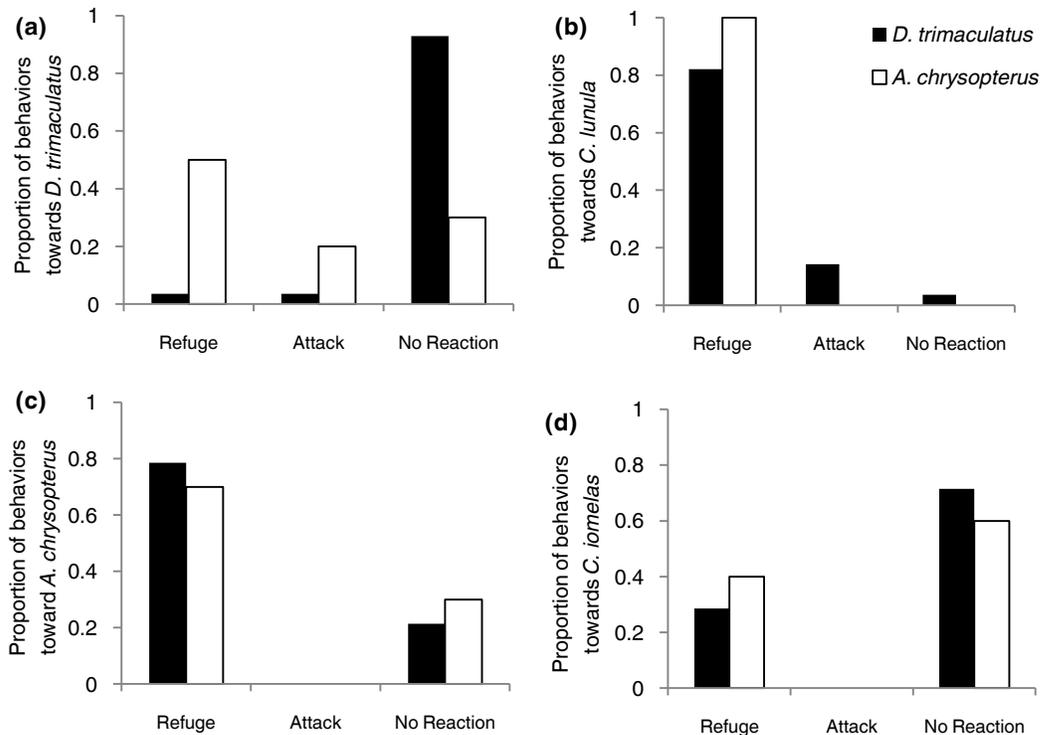


FIG. 5. Behavior reactions of *D. trimaculatus* and *A. chrysopterus* towards the (a) *D. trimaculatus* model, (b) *C. lunula* model, (c) *A. chrysopterus* model, and (d) *C. iomelas* model.

behavior between *A. chrysopterus* and *D. trimaculatus*. As expected, *A. chrysopterus* showed more aggression during pure observation towards neighbors and intruders, but *D. trimaculatus* surprisingly exhibited more aggressive behavior towards the fish models.

Territory size and fish counts

My results for territory sizes were inconsistent with my hypothesis which predicted that *A. chrysopterus* should defend larger territory sizes. Because the difference in adjusted territory size of each species was not statistically significant, territory size could be affected by other factors. The territory sizes were variable within each species, thus other aspects such as population dynamics or environment could have had influenced results. For example, population sizes on the anemone or the absence or presence of *A. chrysopterus* may have affected how far the fish wandered from the anemone. I observed that with the presence of *A. chrysopterus*, the *D. trimaculatus* population on the anemone tended to maintain a larger distance from *A. chrysopterus* and thus appeared to wander further from the anemone. The fish populations and abundances of different fish species that resided and swam near the anemone may also have had an effect on territory size. For example, an environment with a high abundance of predators may have induced the fish to be more aggressive, and thus defend larger territory sizes.

Another source of error could have arisen from how I defined "territory size" – the area the fish wandered may not necessarily be equivalent to the area the fish will defend. I may have measured an area more similar to a home range, in which the fish wandered and fed in, but may not have exhibited territorial behavior throughout this entire area.

The differences in trends between anemone size and number of residents between *A. chrysopterus* and *D. trimaculatus* were due to the differing lifestyles of the fish.

D. trimaculatus uses the anemone only as a nursery, and as expected, the more fish available to defend the anemone resulted in a healthier and larger anemone. In contrast, a maximum of two *A. chrysopterus* can inhabit an anemone, and in my results there was not a clear trend between having zero, one, or two *A. chrysopterus* present on the anemone and the size of the anemone. This is inconsistent with Holbrook and Schmitt's (2005) study in which they found that an anemone with one or two *A. chrysopterus* is significantly larger than an anemone with zero *A. chrysopterus*. Because *A. chrysopterus* relies on the anemone as a lifelong home as well as a safe haven for its egg clutches, it should be especially diligent in defending the anemone and promoting its growth. I had predicted that there would be a strong positive relationship between the number of *A. chrysopterus* present and anemone size, however, this discrepancy could have been due to my small sample size.

My study also only measured anemone size rather than growth which would have required a longer study. Perhaps the relationship between the number of *D. trimaculatus* and anemone size suggests that the anemone size limited the number of *D. trimaculatus* that can settle on the anemone, while the lack of relationship between the number of *A. chrysopterus* and anemone size indicate that anemone size did not limit its population size. This perspective aligns with the fishes' life histories, as a maximum of two *A. chrysopterus* can settle on one anemone, while as many *D. trimaculatus* as possible will settle on an anemone until there is not enough space for fish to take refuge or current tenants successfully chase new settling fish away.

Aggression towards neighbors and intruders

The differences in conspecific and neighbor aggression between *A. chrysopterus* and *D. trimaculatus* can be explained by differing lifestyles and fish size. The absence of conspecific aggression of *A. chrysopterus* is expected because any conspecifics living on

the anemone would be its mate. The high amounts of neighbor aggression of both fish were also expected due to the competition for the same resources. Small *D. trimaculatus* did not attack fish larger than them, resulting in a lower frequency of aggression.

The differences in aggression towards intruders between *A. chrysopterus*, and small and large *D. trimaculatus* can also be explained by differing lifestyles and fish size. *A. chrysopterus* is a long term resident and protects the anemone more rigorously, and is also largest in size. The larger *D. trimaculatus* can afford to pick more fights than the small *D. trimaculatus*.

Aggression towards various fish species

The differences in behavior of *D. trimaculatus* and *A. chrysopterus* towards the varying fish models were due to differing lifestyles on the anemone and perhaps the fishes' awareness. *A. chrysopterus* had high percentages of taking refuge in the presence of the model fish because they seemed to be more aware of my presence. I observed it swimming up and down within the tentacles of the anemones, and it appeared to monitor all surroundings including the area above the anemone. In contrast, from what I observed, *D. trimaculatus* seemed more focused on the surroundings at the depth of the anemone, and did not pay as much attention to what was above them.

Both species took refuge from the *A. chrysopterus* model because *A. chrysopterus* is an aggressive competitor for anemone territory, although I expected *A. chrysopterus* to be aggressive towards an unknown conspecific to maintain its territory. Both species were unreactive towards the *C. iomelas* which was expected because *C. iomelas* is an herbivorous fish that is harmless and commonly grazes algae around anemones.

The *C. lunula* model caused both species to take refuge, which was not what was expected – *C. lunula* is an anemone-eating fish that *D. trimaculatus* and *A. chrysopterus* should be

fighting off to maintain the health of the anemone. Only a few brave *D. trimaculatus* did attack the *C. lunula*, while none of the *A. chrysopterus* dared to approach the model; this may be due to *A. chrysopterus*' awareness to my presence. The size of the *C. lunula* model was also 9 cm across – much larger than both fish species – and the model's large size alone may have scared the fish in study.

Lastly, the *D. trimaculatus* model was generally met by no reaction by the *D. trimaculatus* which was expected, as the model appeared like another neighbor. *A. chrysopterus* unexpectedly took refuge, but this behavior may have also been induced by my presence. A few *A. chrysopterus* did attack the model, however, which was the expected behavior because *A. chrysopterus* should be minimizing the number of neighbors in its territory.

The fish models seemed successful in gauging the behaviors of *D. trimaculatus*. However *A. chrysopterus* usually behaved towards the fish models similarly to how it behaved to my presence, making this method less effective for assessing its behavior. Through this observation, I am still able to show that the species differ in awareness to their surroundings. The higher awareness of *A. chrysopterus* may suggest that it is more alert than *D. trimaculatus* and is able to defend the anemone more effectively.

CONCLUSIONS

This project showed that *A. chrysopterus* was more aggressive during the purely observational studies towards neighbors and intruders than *D. trimaculatus*. However, although *D. trimaculatus* appeared to be more aggressive towards the fish models, my presence may have had an uneven affect on each species of fish which may have skewed results. This study brings light to more areas of heterospecific agonistic behavior that must be studied and underlines how crucial and difficult it is to control for factors that may influence results.

Future studies can include a more thorough examination of behaviors towards a wider variety of species with the fish models to detect differences in heterospecific aggression in *D. trimaculatus* and *A. chrysopterus*. Looking into quantifying the awareness of each species would also be valuable to understanding how the fish react and interact with its surroundings. It would be beneficial to study similar systems in which two species are competing for the same resources and are forced to interact. For example, studies can be done on different species of birds compete for nesting space, or how encrusting corals and bryozoans compete for growing space on rocks. Comparing their territorial behaviors would contribute to a better understanding of heterospecific interactions as well as how each species affects the dynamics of the community.

The results I achieved from this study, especially the unexpected ones, are evidence that the uncertainties between species make heterospecific agonistic behavior complex, yet still possible to quantify and study. The prevailing aggression of *A. chrysopterus* towards neighbors and intruders exemplify how it is the dominant mutualist over *D. trimaculatus*, which affects dynamics within the anemone community as well as the reef community in the system. At a larger scale, It is important to keep studying every aspect of animal behavior, including the complex and bewildering aspects such as heterospecific agonistic behavior that also influence community structure. This is crucial to understanding and appreciating the complex web of relationships between species in ecosystems which is ultimately necessary to preserve the spectacular biodiversity of the reefs of Mo'orea as well as the rest of the world.

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LITERATURE CITED

- Brawley, Susan H., Adey, Walter H. 1977. Territorial behavior of threespot damselfish (*Eupomacentrus planifrons*) increases reef algal biomass and productivity. *Environmental Biology of Fishes* **2**: 45-51.
- Connell, Joseph H. 1963. Territorial behavior and dispersion in some marine invertebrates. *Researches on Population Ecology* **5**: 87-101.
- Dhaneesh, K. V., Ajith Kuma, T. T., Shunmugaraj, T. 2009. Embryonic Development of *Percula Clownfish, Amphiprion percula* (Lacepede, 1802). *Middle-East Journal of Scientific Research* **4**: 84-89.
- Fautin, Daphne Gail 1991. The anemonefish symbiosis: what is known and what is not. *Symbiosis* **10**: 23-46.
- Fretwell, Stephen Dewitt, Lucas, Henry L. 1963. On territorial behavior and other factors influencing habitat distribution in birds I. Theoretical development. *Acta Biotheoretica* **19**: 16-36.
- Goodman, Donald E. 1971. Territorial Behavior in a Neotropical Frog, *Dendrobates granuliferus*. *Copeia* **2**: 36-370.
- Graf, William 1956. Territorialism in deer. *Journal of Mammalogy* **37**: 165-170.
- Holbrook, Sally. J., Schmitt, Russell. J. 2004. Population dynamics of a damselfish: effects of a competitor that also is an indirect mutualist. *Ecology* **85**: 979-985.
- Holbrook, Sally. J., Schmitt, Russell. J. 2005. Growth, reproduction and survival of a tropical sea anemone (Actiniaria): benefits of hosting anemonefish. *Coral Reefs* **24**: 67-73.

- Katzir, Gadi 1981. Aggression by the damselfish *Dscyllus aruanus* towards conspecifics and heterospecifics. *Animal Behavior* **29**: 835-841.
- Krebs, J. R., Davies, N. B. *Behavioural Ecology: An Evolutionary Approach*. Third Edition. New York: Blackwell Scientific Publications, 1991. Print.
- Krebs, J.R., Davies, N. B. *An Introduction to Behavioral Ecology*. 2nd Edition. Oxford: Blackwell Science Inc, 1987. Print.
- Meyer, J.L., Schultz, E.T. 1985. Migrating haemulid fishes as a source of nutrients and organic matter on coral reefs. *Limnology and Oceanography* **30**:146-156.
- Mitchell, J.S. 2003. Mobility of *Stichodactyla gigantea* sea anemones and implications for resident false anemonefish, *Amphiprion ocellaris*. *Environmental Biology of Fishes* **66**: 85-90.
- Moyer, Jack T., Sawyers, Claire E. 1973. Territorial behavior of the anemonefish *Amphiprion xanthurus* with notes on the life history. *Japanese Journal of Ichthyology* **20**: 85-93.
- Moyer, Jack T. 1986. Longevity of the Anemonefish *Amphiprion clarkii* at Miyake-Jima, Japan with Notes on Four Other Species. *Copeia* **1**: 135-139.
- Peiman, Kathryn S., Robinson, Beren W. 2010. Ecology and evolution of resource-related heterospecific aggression. *The Quarterly Review of Biology* **85**: 133-158.
- Porat, D., Chadwick-Furman, N. E. 2004. Effects of anemonefish on giant sea anemones: expansion behavior, growth, and survival. *Hydrobiologia* **530/531**: 513-520.
- Shima, Jeffrey S. 1992. Territory structure and aggregated behavior of damselfish (*Stegastes nigricans*) on Moorea, French Polynesia. *The Biology and Geomorphology of Tropical Islands Student Research Papers*, Fall 1992: 268-284.
- Vandermeer, John H., Boucher, Douglas H. 1978. Varieties of Mutualistic Interaction in Population Models. *Journal of Theoretical Biology* **74**: 549-558.