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INTERSPECIFIC COMPETITION BETWEEN CONTAINER SHARING MOSQUITO LARVAE, *Aedes aegypti* (L.), *Aedes polynesiensis* MARKS, AND *Culex quinquefasciatus* SAY, IN MOOREA, FRENCH POLYNESIA

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Abstract. The interspecific competition between three container sharing mosquitoes was investigated to further understand the reasoning for ovipositing partitioning previously analyzed. Past studies have demonstrated distinct difference in larval use of containers between *Aedes aegypti* and *Aedes polynesiensis*, preferring artificial and natural containers, respectively. Additionally, *Culex quinquefasciatus* is present in both types of containers. It was hypothesized that this partitioning was the result of interspecific competition between the species. To analyze this, two treatments were conducted to induce competition; food limiting (between *Ae. aegypti* and *Ae. polynesiensis*) and space limiting (between all three species), with the emergence rates being the calculated variable. ANOVA tests revealed that when food is present, *Ae. polynesiensis* competes better interspecifically than intraspecifically, suggesting that competitive displacement occurs in natural containers. It was also found that a space limiting environment does not provide a statistical significant difference between the emergence times of *Ae. aegypti*, *Ae. polynesiensis*, and *Cx. quinquefasciatus*, providing that larval density does not induce competition between these three species and therefore cannot be used to analyze theories for ovipositing partitioning.

Key words: *Aedes polynesiensis*, *Aedes aegypti*, *Culex quinquefasciatus*, larval competition, interspecific competition, emergence rates, competitive exclusion, mosquito.

INTRODUCTION

Mosquitoes in French Polynesia have been longstanding pests, particularly in their transmission of disease. *Aedes aegypti*, the yellow fever mosquito, a vector for Dengue fever, and *Aedes polynesiensis*, the Polynesian tiger mosquito, a vector of *Wuchereria bancrofti* (the parasite leading to lymphatic filariasis resulting in elephantiasis), are the two major vector-mosquitoes in Moorea, and well studied pests (Gubler, 1988; Rosen, 1955). The third species present in this study is the locally non-vector *Culex quinquefasciatus*; worldwide *Cx. quinquefasciatus* is a vector of West Nile virus; however this disease is not currently present in Moorea. *Cx. quinquefasciatus* is still equally important to study as it tends to share the same habitats as the *Aedes* genera mosquitoes (Becker, 1995; Russell, 2004; Hribar, 2007).

The impact of mosquito-borne illnesses is increasing as these vectors spread further into subtropical and tropical environments and species are becoming better adapted to a variety of conditions (Hammond *et al.*, 2007.) Particular efforts have been established to combat the spread of lymphatic filariasis; with the goal of stopping the transmission of this disease in the 16 Pacific island countries and territories where it is present, the Pacific Program for the Elimination of Lymphatic Filariasis was established (Burkot & Ichimori, 2002; Burkot *et al.*, 2002). The program's current effort in the French Polynesian islands is to combine a program of mass drug administration and species eradication programs to completely rid the islands systems of *Ae. polynesiensis* and rid the human population of the respective parasite *Wucheraria bancrofti* (Cobbold).

An issue that arises with all species eradication programs is the biodiversity impacts,

in particular the newly formed habitat resources present to other competing species. Tilman (1982) defines resource as “any substance or factor which is consumed by an organism and which can lead to increased growth rates as its availability in the environment is increased”. competitive exclusion principle. If two similar species are unable to coexist in the same niche, then it can be assumed that they are too similar in their resource consumption, i.e. one is outcompeting the other for resources, and competitive exclusion occurs (Hardin 1960).

For *Ae. polynesiensis*, one of the major resources that will be freed as a result of its eradication will be the larval habitats where mosquitoes oviposit. The aquatic larvae of *Ae. polynesiensis*, *Ae. aegypti*, and *Cx. quinquefasciatus* inhabit water-filled containers, receiving nutrients from microorganisms and other fine particulate food present in the water column (Braks *et al.*, 2004). However, *Ae. polynesiensis* and *Ae. aegypti* do not coexist in containers on Moorea. The breeding preferences of *Ae. polynesiensis* are those of natural containers (e.g. coconuts, crab holes, etc.) (Bonnet & Chapman, 1958), whereas *Ae. aegypti* prefers artificial containers (e.g. potting plants, empty cans and bottles, etc.), while *Culex quinquefasciatus* prefers both types of habitats (Russell & Richie, 2004; Burkot *et al.*, 2007).

Juliano (1998) proposed that interspecific resource competition is the most viable rationale for the observed decline of *Ae. aegypti* presence in the United States, having been outcompeted by another species from its genera, *Ae. albopictus*. Both this experimental evidence and the theory of coexistence demonstrate that resources affect the outcome of competition. The goal of this project was to determine whether or not lack of coexistence in natural and artificial containers was the result of interspecific competition between the larvae of these species. Two major resources that provoke competition in all systems are nutrients and space. The mechanism of such an interaction is classified as exploitation competition, which occurs when the effects of one species on another are indirect, specifically through the reduction of the present pool of resources (Keddy, 1989). The first study analyzed limiting food while the second study limited space, specifically the volume of water per larva. Three parameters were examined to quantify the effects of competition; time of emergence of adults from the larval stage,

Resources are the fundamental factors that influence the organization of communities (Price, 1984). The existence of two closely related species in the same niche sharing the same resources is a theory associated with the

number of adults emerging, species of adults emerging.

MATERIALS AND METHODS

Larvae collection

Larvae utilized in this study were collected from various field locations. *Ae. aegypti* larvae were collected from two outrigger canoes located at the Gump Station located on the Eastern end of the station; one was located next to the boat storage on the water, approximately 5 yards from the closest human inhabitation, while the other was located next to the cabana on the water approximately 15 yards from the closest human inhabitation. Larvae were collected on November 4th for both the food limiting experiment and space limiting experiment. Larvae collected from the outriggers were pipetted into 90 ml plastic cups for transportation to lab. *Ae. polynesiensis* larvae were collected from coconuts at two locations; Opunahu Coconut Grove located on the north side of the island between PK 14 and 15, and the Vaiare Coconut Grove located on the eastern side of the island between PK 5 and PK 6. Rat-chewed coconuts were examined for the presence of water, and if present was poured into an 11 inch by 12 inch metal tin to determine whether or not larvae were present (fresh water was used to dilute murky water for a clearer visual). If larvae were present, water and larvae were poured into 90 ml plastic cups organized by coconut for transport to the lab.

Larval age was estimated based on size of larvae, and only the smallest larvae were kept so that they would be starting at the earliest points of their larval stage.

Food limiting experiment

The experiment was conducted in the “wet lab” located at the Richard B. Gump Station in Cooks Bay, Moorea, French Polynesia. Mosquito larvae collected from the field were pipetted into white, plastic cups (8 cm in height, 3 cm base diameter) that were utilized as the

larval containers. In each container there were a total of 20 larvae, and each cup contained 100 ml of fresh water. All cups were covered with a six inch by six inch square of fine green or gray mesh situated with a rubber band to catch adults as they emerge as well as to prevent oviposition mg of Tetramin (fish food) per larvae per day. Food was delivered in dry form and sprinkled over the top of the cup.

There were six treatments total. For *Ae. aegypti* intraspecific competition there were two treatments; *Ae. aegypti* with food and *Ae. aegypti* without food. For *Ae. polynesiensis* intraspecific competition there were also two treatments; *Ae. polynesiensis* with food and *Ae. polynesiensis* without food. For the interspecific competition between *Ae. aegypti* and *Ae. polynesiensis* the two treatments were both species together with food (ten *Ae. aegypti* and ten *Ae. polynesiensis*), and finally both species without food (ten *Ae. aegypti* and ten *Ae. polynesiensis*). There were seven replicates for each treatment for a total of 42 containers and 840 larvae

Containers were examined on a daily basis for approximately 18 days, until November 21st. Intra- and interspecific larval competition was studied by monitoring the number of live larvae, pupae, and adults, as well as the number of deceased larvae, pupae, and adults present in each cup daily. When adults emerged they were identified, sexed, numbered, and day of emergence was recorded. At the end of the experiment the total number of individuals emerged was noted for each cup, as well as their species.

Two two-way ANOVAs were utilized to analyze the effects of intra- and inter-specific competition on each mosquito species; one two-way ANOVA for *Ae. aegypti* and one two-way ANOVA for *Ae. polynesiensis*. The emergence rate of each species from each cup was calculated. Next, the model effects were determined to be either the presence or absence of food and either intra- or inter-specific competition, with the y-variable being *Ae. aegypti* emergence rate for the first ANOVA, and the y-variable being *Ae. polynesiensis* emergence rate for the second ANOVA.

Space limiting experiment

The experiment was also conducted in the “wet lab” located at the Richard B. Gump Station

by wild mosquitoes. Cups were labeled (columns denoted with a number and demonstrating treatment, and rows labeled with numbers and representing replicate). Cups were placed in a large table located in the open air wet lab. Treatments requiring food received 0.06 in Cooks Bay, Moorea, French Polynesia. Mosquito larvae collected from the field were pipetted into white, plastic cups (8 cm in height, 3 cm base diameter) that were utilized as the larval containers. In each container there were a total of 20 larvae, 10 from a natural container (presumed to be *Ae. polynesiensis* with potentially *Cx quinquefasciatus*) and 10 from an artificial container (presumed to be *Ae. aegypti* with potentially *Cx. quinquefasciatus*). All cups were covered with a six inch by six inch square of fine green or gray mesh situated with a rubber band to catch emerging adults as well as to prevent oviposition by wild mosquitoes. Cups were labeled (columns denoted with a number and demonstrating treatment, and rows labeled with numbers and representing replicate). Cups were placed in a large table located in the open air wet lab. Food, 0.06 mg of Tetramin (fish food) per larvae was delivered on a daily basis. Food was delivered in dry form and sprinkled over the top of the cup.

The six treatments were; 2 ml of water/larvae, 3 ml of water/larvae, 4 ml of water/larvae, 5 ml of water/larvae, 6 ml of water/larvae, and 7 ml of water/larvae. There were six treatments with five replicates for each treatment, for a total of 30 containers and 600 larvae.

Each container was monitored daily for approximately 18 days, until November 21st; the number of live larvae, pupae, and adults were recorded, as well as deceased larvae, pupae, and adults. When adults emerged they were identified, sexed, and the number were recorded. At the end of the experiment the total number of individuals emerged was noted for each cup, as well as their species.

For analysis of the differences between the emergence times of the three mosquito species, three one-way ANOVA tests were conducted. The model effects for all three ANOVAs were treatment (volume of water) and emergence day, with the y-variable being one of the three species.

RESULTS

Food limiting experiment

Table 1. Two-way ANOVA results for emergence rates of *Ae. aegypti* and *Ae. polynesiensis*.

Source	Emergence Rates					
	<i>Ae. aegypti</i>			<i>Ae. polynesiensis</i>		
	df	F	P	df	F	P
Presence of Food	1	250.842	<.0001	1	456.188	<.001
Competition	1	0.442	0.5126	1	0.542	0.4686
Food × Competition	1	0.006	0.9417	1	6.919	0.0147

The first two-way ANOVA conducted with *Ae. aegypti* yielded an r-square value of 0.910, demonstrating that the yield had minimal variation. The remaining variation had a standard error of 0.128. All effects had 1 degree of freedom. An F-value of 250.82 and a *p*-value of <0.001 were yielded for the presence of food. An F-value of 0.442 and *p*-value of 0.5126 were generated for the competition effect. The interactions between presence of food and competition produced an F-value of 0.006 and a *p*-value of 0.9417 (Table 1). Therefore, the data does not show a statistical difference between the performances of *Ae. aegypti* under intraspecific vs. interspecific competition.

The second two-way ANOVA performed on *Ae. polynesiensis* generated an r-square value of 0.951, explaining much of the variation in the yield. The remaining variation had a standard error of 0.089. All effects had 1 degree of freedom. The F-value was 456.188 and the *p*-value was <0.0001 for the presence of food, whereas the F-value was 0.542 and the *p*-value was 0.4686 for competition. However, a statistically significant *p*-value of 0.0147 (highlighted in Table 1) was also yielded (F-value was 6.919) for the interactions between competition and food, the variable most important in this study, showing evidence that the model adequately captured most factors present in this response (Table 1). This revealed that under a higher stress environment (food absent) *Ae. polynesiensis* performs better against itself (intraspecific comp.) rather than against *Ae. aegypti* (interspecific comp.). However, under a less stressful environment (food present) *Ae. polynesiensis* performs better against *Ae. aegypti* (interspecific comp.) rather than against itself (intraspecific comp.)

Space limiting experiment

The pattern of results from all three ANOVAs conducted did not find a significant relationship between species and emergence rates. *Ae. aegypti* yielded an r-square value of 0.232, with the remaining variance having a standard error of 0.591, demonstrating that there is a significant amount of variation in the yield. The significant lack-of-fit test, a *p*-value of 0.4661, with 5 degrees of freedom and an F-value of 1.689, shows evidence that there is something in the factors that is not being accounted for in the model, and the model is more complex than demonstrated. *Ae. polynesiensis* generated similar results with an r-square value of 0.055 and a root mean square error of 0.682. The results had 5 degrees of freedom, an F-value of 1.399, and a *p*-value of 0.7003. *Cx. quinquefasciatus* was also similar, producing an r-square value of 0.042, a root mean square error or 0.699. The results also had 5 degrees of freedom, an F-value of 2.269, and a *p*-value of 0.4654 (Table 2).

DISCUSSION

Food limiting experiment

My results show that when food was present, *Ae. polynesiensis* had a greater emergence rate when in a container with *Ae. aegypti* as opposed to a container with only *Ae. polynesiensis*. However when food was not present, *Ae. polynesiensis* had a greater emergence rate when in a container with only *Ae. polynesiensis* as opposed to a container with *Ae. aegypti*. That is, the results indicate that *Ae. polynesiensis* competes better against *Ae. aegypti* (interspecifically) when food is present, however when food is not present *Ae. polynesiensis*

competes better against itself (intraspecifically) (Figure 1a and 1b). The analysis is similar for

Table 2. ANOVA results for emergence day for *Ae. aegypti*, *Cx. quinquefasciatus*, and *Ae. polynesiensis*.

Source	Emergence Day								
	<i>Ae. aegypti</i>			<i>Cx. quinquefasciatus</i>			<i>Ae. polynesiensis</i>		
	df	F	P	df	F	P	df	F	P
Model	5	1.689	0.9682	5	2.269	0.9290	5	1.399	0.5997
Error	16	5.583	0.4661	105	51.30	0.4654	52	24.208	0.7003

Ae. aegypti; given that artificial containers would not necessarily provide an abundance of nutrients, therefore providing a more stressful situation with the absence of food, *Ae. aegypti* would be less likely to be outcompeted by *Ae. polynesiensis* in these environments, and therefore would prefer to oviposit in such containers. *Space limiting experiment*

The lack of a significant relationship demonstrated between the emergence rates of the different species still provides implicative results. Given that there was not a significant difference in the emergence days of the three mosquito species based on the volume of water, it can be suspected that larval density is not a variable in the container environment that induces competition between the three species.

Nonetheless, these results might also be explained by examining the confounding variables that were present such as; location, larval stages, and larval abundances. The location of the experiment was conducted outdoors, therefore leaving the experiment exposed to such variables as wind, temperature, varying photoperiods, and uncontrolled evaporation. Additionally, when the different larvae were collected in the field, despite efforts to age them by size, there was still that variation present, which, given the relatively short periods for emergence, would highly influence the data.

My results are dissimilar to that of previous research which demonstrated that increasing larval density also increases mortality rates in the larval stages (Gama *et al.*, 2005). Some of the contradictory conclusions could have resulted from a series of differences. Though interpopulation differences in life history traits leading to competition are not generally observed, there have been cases of this occurring between

varying geographic strains of the same species. Livdahl (1984) demonstrated differences in composite index of performance between different geographic strains of *Ochlerotatus triseriatus* (Say) in the United States. He suggested that the variability in prevalence of predation by *Toxorhynchites rutilus* (Coquillet) evolved differences in growth rate and competitive ability as a result of differences in effective predator avoidance mechanisms. The Gama *et al.* (2005) study that I compared my results to was conducted with a Brazilian strain of *Ae. aegypti* whereas my strain originated from Moorea.

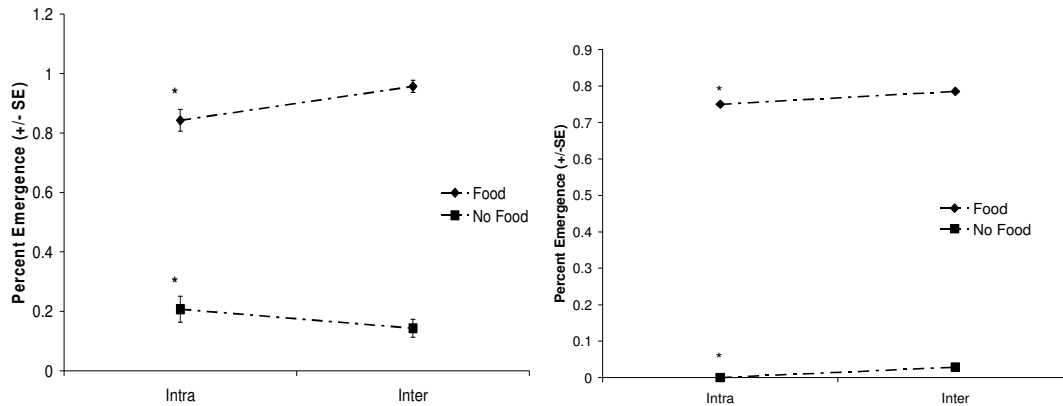
Additionally, my study was conducted at lower larval densities than previous studies. Despite the ratios of water to larva being similar, other studies were conducted with larvae counts in the upper 200s, however my study was done at a much smaller larval density, but similar ratios. An interesting explanation could also be the differences in the exposed surface area; larva require oxygen and can commonly be found floating on the top of the water source. Consequently, my containers may have provided an efficient amount of surface area for this resource to not be limited and therefore result in a smaller mortality rate.

As a result of the lack of conclusive data from the space limiting experiment, this resource will not be included in the following discussions.

Competitive advantage

Competitive advantage is achieved by the species demonstrating continuous or increased growth, whereas its competitor exhibits population decline (Pianka, 1988). The results of this study show evidence that when food is present, *Ae. polynesiensis* has the competitive advantage over *Ae. aegypti*. Applied to the

Figure 1. Effects of presence of food on the percent emergence between intra- and inter- specific competition of a) *Ae. polynesiensis* and b) *Ae. aegypti*



* In the analysis of this figure, it is not the slope of the two series but rather the difference in the location of the indicators between intra- and inter- specific competition.

Observed relationships in the field, this theory appears appropriate. Natural containers that *Ae. polynesiensis* is commonly found in (coconuts, palm fronds, and crab holes) biologically provide an abundance of nutrients; by nature species would prefer to reside in these habitats. However, based on the results of this experiment, it would be assumed that *Ae. polynesiensis* would outcompete *Ae. aegypti* for this niche, and this is exactly the pattern that is demonstrated in the field with *Ae. polynesiensis* present in the natural containers and *Ae. aegypti* present in artificial containers.

It is necessary to acknowledge that *Ae. polynesiensis* does not exclude *Ae. aegypti* completely from the system. That is, that *Ae. aegypti*, despite not being able to coexist in the larval habitats, is still able to coexist in the overall habitats. Hardin (1960) summarizes this as an 'ecological differentiation'. The two species may be too similar to allow coexistence in the larval stage, however they are able to find a level of coexistence in the adult stage and system. This theory is demonstrated in this study; the results provided evidence that *Ae. aegypti* is outcompeted only when food is present, so it has managed to inhabit a container that does not provide an abundance of nutrients and therefore would not induce competition that would inevitably exclude from this container as well.

Bedhomme *et al.* (2003) discusses the fitness consequences of differences in a particular life-history trait are not necessarily the same for the

both species. While *Ae. polynesiensis* is native to the South Pacific, *Ae. aegypti* is a non-native species having originated in Africa (Kahmhampti & Rai, 1990; Mousson *et al.*, 2005) Consequently, *Ae. polynesiensis* would be genotypically and phenotypically more evolved to this environment, developing particular life-history traits that allow to adequately utilize resources and evolve to the abiotic and biotic conditions of the environment. This combination of population origin and adaptation to the local environment would allow *Ae. polynesiensis* to outcompete *Ae. aegypti* upon its arrival.

Species eradication implications

Furthering our understanding of the ovipositing and breeding sites of these mosquito species is imperative to develop efficient vector-control and species eradication programs that will not harm the system or, in this case, potentially influence the spread of another vector-mosquito, *Ae. aegypti*.

The implications of this study for the proposed eradication of *Ae. polynesiensis* potentially demonstrate that such an eradication program could provide more viable habitats for the spread of *Ae. aegypti*. Provided that, as the evidence supports, *Ae. polynesiensis* outcompetes *Ae. aegypti*, the removal of this species from the system could remove this competitive exclusion from *Ae. aegypti* and potentially encourage it to expand to areas with more abundant nutritional resources, natural

containers. The potential influence that this has on the region is an increase in the rate of dengue fever across the region. This eradication program would therefore be replacing a high abundance of one disease with another.

This situation is delicate given that this eradication program is of a disease vector that is damaging the lives of many people in French Polynesia, as well as elsewhere around the world. The goal of the program is to eradicate a disease that hinders the lives of many. Once the elimination of the parasite from the human population is complete, it is expected that the unaffected species will be reintroduced, therefore returning the system to its initial state. With this in mind, the eradication program has the habitat and influence environment in mind with its program management.

Species eradication programs commonly target invasive species, not native species. As a result, there has been minimal research on the consequences of removing a native species from its habitat. Consequently, further research is required to determine the full affects of the removal of *Ae. polynesiensis* from the Moorean habitat.

Future research

Future research is required to further understand the interactions and relationships occurring within and between these species and containers. This experiment could be repeated under more controlled environments in a laboratory, and with a significantly larger sample size to account for more variance. Additionally, future research would benefit from utilizing a laboratory grown strain of larvae to account for exact age and species. Further research conducted should analyze other variables that induce competition, such as water temperature and light tolerance. To further research the implications of eradication *Ae. polynesiensis*, other species present in the system that can influence the resource exploitations should be analyzed to understand the balance of the system and how that would be affected.

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