BOLDNESS AND EXPLORATORY BEHAVIOR OF THE GUPPY, *POECILIA RETICULATA*, IN MOOREA, FRENCH POLYNESIA

RUTH JEAN AE KIM

Integrative Biology, University of California, Berkeley, California 94720 USA

Abstract. The frequent spread of invasive species has increased since the modernization of human transportation and commerce. Key in the success of an invasive species is its ability to disperse, spread and establish as a sustainable population within a new environment. There has been a trend in invasion ecology that hypothesizes that one of the mechanisms of invasive species' success is their behavior. *Poecilia reticulata*, guppy, is an invasive freshwater fish in Moorea, French Polynesia. Past studies have shown Poeciliids have displayed bold and aggressive behavior, which may indicate success in novel environments. In this study, the correlation of invasiveness, boldness and exploratory behavior was examined. Male guppies are bolder than female guppies, while exploration behavior did not differ between the sexes. In the presence of a predator *Macrobrachium spp*., males were less bold with visual and chemical treatments and females were bolder under treatments of visual and visual and chemical treatments. Exploration behavior between the two sexes also did not differ. Overall there was no significant difference between sexes with the predator study. Surveys also suggest guppies are spread throughout the freshwater systems of Moorea. Understanding the relationship between sex, boldness and exploratory behavior when encountering novel environment and predator, give insight into the mechanisms of successful invaders.

Key words: Poecilia reticulata; boldness; exploratory behavior; invasive *; Moorea, French Polynesia; Macrobracium spp.; behavioral syndromes*

INTRODUCTION

Human activities have altered the composition and dynamics of ecosystems on a global scale. A consequence of these activities is the rapid spread of invasive species. An invasive species is one whose geographical range is spreading away from their native range (Vermeij 1996). Continents, islands, and oceans have been affected by invasive species, raising the importance of understanding how and why it occurs (Elton 1958). Organisms are able to reach new habitats across continental barriers due to human impacts of agriculture, aquaculture, transportation and commerce (Kolar and Lodge 2001). Making humans key dispersal agents, increasing the frequency and number of biological invasions for the past 500 years (Mack et al 2000).

Introductions can be intentional or unintentional and their impacts relate to economic, ecological, and health issues (Vitousek 1997). For example, the zebra mussel has become widespread in the North American Great Lakes, accidentally introduced through ship ballast. Due to the established population of the zebra mussel, the endangered native clam population has declined (Lodge 1993). The introduction and spread of the African mosquito in 1929 in Brazil, caused outbreaks of malaria affecting hundreds of thousands of people (Elton 1958).

Accumulating invasive species have been able to adapt and compete with native organisms through niche displacement, predation and competition. Successful invaders must be able to establish themselves and sustain a stable population. Traits of successful invaders include r-selected strategies often in association with both human-impacted and natural environments (Sax 2000). Invasion is a process with stages of introduction, establishment and spread (Lodge 1993). Characters that make these stages possible are worth investigating. An organism should be able to interact with the community it must survive in. Behavior is an important aspect of invasion. The concept of *behavioral syndromes* relates to the success an individual can possess within certain contexts. For example, an individual with an aggression syndrome may benefit at times of competition but may suffer in time in need of caution (Sih et al 2004).

Behavioral flexibility relates to a species' capability of adapting to new contexts and niches such as food and space (Wright et al 2010). Behavioral plasticity and in particular, aggressive or bold behavior may contribute to

an invasive species' ability to establish itself (Lodge 1993, Sih et al 2004, Suarez et al 2001). Invasive species have been able to exploit resources and reproduction compared to native species for example with geckos, argentine ants, mosquitofish (Short and Petran 2008). Previous studies have found that organisms that are willing to try new sources of resources are usually invasive and therefore, attain more than their counterpart natives. (Sol et al 2002) Furthermore, an invasive species' ability to respond to biotic factors such as predators in the region can aid the success of the invader (Shea and Cheson 2002). Other ecologically relevant behaviors include high dispersal rates which in turn correlate with boldness and high activity which give rise to invaders that are able to insert themselves into the community structure (Fraser et al 2001, Sih et al 2004).

Dispersal to remote areas of the world has created the biggest proportion of invasive species on islands (Mooney and Cleland 2001). Characteristics of islands that make them prone to invasion are their geographic isolation, taxonomic disharmony and low diversity in comparison to the mainland (Carlquist 1974). Because of these unique aspects of islands, human destruction and introductions make indigenous species on islands more prone to extinction. (Atkinson 1989). There have been instances of fish extinctions due to the introduction of the brown trout in New Zealand in the 1800s (Mooney and Cleland 2001). Moorea has 37 native freshwater fish species, 2 are invasive freshwater species. The Poeciliidae fish family, particularly the guppy *Poecilia reticulata*, has been used as a biological control for mosquitos, in order to prevent the spread of malaria in tropical countries. In addition, these fish are often released into natural environments from home aquaria (Jourdan et al 2014). *Poecilia reticulata*, originates from South America and was introduced to the Society Islands in 1920 (Marquet 2002). They are a live-bearing fish species Guppies are also sexually dimorphic Males are 2.5 cm to 3 cm long while females are 4 cm to 7 cm long. Males also display polymorphisms in coloration that is beneficial for sexual selection. On the other hand, females are drab and uniform in coloration (Reznick and Endler 1982).

Past studies have used the Poeciliidae family as the subject of experiments relating to invasiveness, boldness and activity (Cote et al 2009, Rehage et al 2004). Parameters of boldness and activity are related to novel-seeking behavior and ability to move in an unfamiliar place (Fraser et al 2001). They specifically used mosquitofish that were used as a biological control for mosquitos. They found a positive correlation between boldness and exploratory behavior. They also found that there were behavioral differences between sexes in their different parameters such as boldness. Males were bolder than females, however females had a higher exploration tendency compared to males. Other past studies have suggested that the boldness behavior of guppies relates to their dispersal ability in the wild (Fraser et al 2001, Budaev 1997).

The effects of predation on guppy behavior have also been considered in past studies. In exposure to predation, a comparison was made between lower predation sites and higher predation sites with Trinidadian guppies. The study found fish that have dealt with one kind of predator do not necessarily benefit when interacting with a novel predator. Furthermore, fish may not be as cautious in new conditions where the level of danger is unknown (Magurran and Seghers 1990). In addition, another study investigating the response of invasive mosquitofish to a novel predator found that there was no response for one species, and decreased foraging and increase refuge use for another invasive species.

In this study, I focused on the guppy, *Poecilia reticulata*, found in the streams of Moorea. In addition, this study serves as an initial survey of Poecilia reticulata within the Opunohu and Pao Pao watershed in Moorea. In the past, there had been a study of freshwater fishes in Moorea, including the feeding behavior of *Poecilia reticulata* however the results for the guppy were not conclusive (Resh et al 1999). I wanted to investigate the dynamics of invasiveness and behavior, specifically, the boldness and exploratory behavior of these guppies. The study investigates (1) whether there was a difference between male and female guppies in their boldness and exploratory behavior (a) whether size is a factor and (2) how a predator affects the boldness and exploratory behavior of male and female guppies (a) what are mechanisms behind predator response: visual chemical or both.

I hypothesized male guppies would be more bold and exploratory compared to female guppies because of their smaller size and their need to mate. Smaller individuals also tend to have higher metabolic rates and therefore may be more inclined to go out to forage in the wild,

which may be reflected in the behavioral assays. Therefore, size would also play a role in boldness and exploratory behavior (Cote et al 2009). I also hypothesized that both male and female guppies would have lower boldness and exploratory behavior scores in the presence of a predator in comparison without a predator.

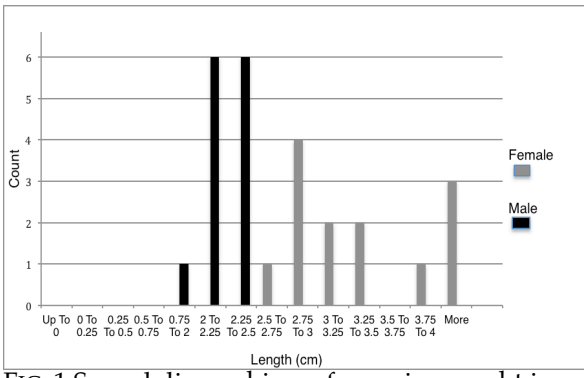

FIG. 1 Sexual dimorphism of guppies caught in Moorea, French Polynesia

METHODS

Collection Sites

Collection sites were conducted at several watersheds on Moorea. French Polynesia. Guppies were collected at the Opunohu watershed, (S 17°31.543′, W 149°50.199′) by the open bridge and (S 17°31.536′, W 149°50.003) by the culvert bridge, and were collected at the Pao Pao watershed, (S 17°30.877′, W 149°49.419′) by Are's market and (S 17°30.925′, W 149°49.911′) by a pineapple plantation.

Fish Collection

All fish collection occurred on the island of Moorea, French Polynesia. The guppy, Poecilia reticulata was sampled and caught. Sampling for this study was done from October until November. Guppies were collected 25m downstream and 25m upstream from the drop off point from each collection site. They were caught with a net and placed in buckets with bubblers and air holes and were then transported to the Gump station where they were placed in tanks filled with aerated stream water. The guppies were identified using a dichotomous key and were checked using a microscope looking for the trait of at least 8-10 anal fin rays. Females and males were identified based on their morphological differences. Males are colorful and smaller while females are larger and lacking coloration. The collected guppies were then measured for their size with a ruler and petri dish. After collection guppies were returned to their respective locations of capture. All work was followed for the UC Berkeley Animal Use Protocol T042-0814.

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Prawn Collection

All prawns, *Macrobracium spp*. were captured using a seine net at site 4 upstream and downstream. The method of kicking up the prawns while running to the seine while 2 people hold the seine net was effective. Prawns were then collected in buckets and taken back to the Gump station where they were placed in aerated stream water.

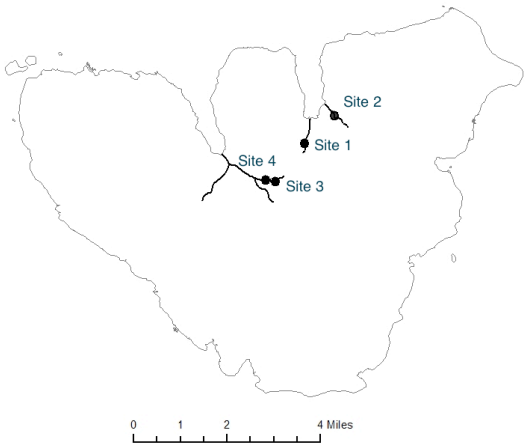


FIG. 2 Map of collection sites and survey locations on Moorea, French Polynesia. Site 1 is S 17°30.877′, W 149°49.419′ (by Are's market) , Site 2 is S 17°30.925′, W 149°49.911′ (by pineapple plantation), Site 3 is S 17°31.536′, W 149°50.003 (culvert bridge) and Site 4 is S 17°30.877′, W 149°49.419′ (open bridge) The map was made using the ArcGIS program.

Experiment: Boldness and Exploratory

I measured the boldness of 15 wild male guppies and 15 wild female guppies. To measure boldness and exploration behavior in a new environment, one fish was tested at a time. The apparatus would consist of a clear glass tank, 53cmx46cmx23cm with freshwater

circulation. In addition, 4 cm of the tank filled with freshwater. An initial refuge site was made of pvc piping (grey in coloration) about 10cm in diameter for the fish to be placed in. The pvc piping had a 4cm wide hole with an outer lining of pvc piping to block the entrance. A string was used to lift the pvc pipe door in order to prevent any disturbance to the organism. The door was lifted for the fish to enter through once it had acclimated to the pvc piping enclosure after 20 minutes. Acclimation time was determined after various tests that were performed to quantify the best amount of time. All methods for this part of the study followed the methods of (Cote et al. 2010).

A grid made of waterproof paper was placed at the bottom of the tank consisting of 4cmx4cm blocks that would be used to visually quantify how far the fish had moved during the trial. A camera apparatus was placed above the tank that recorded the trials so that further analysis could be done. A black curtain was placed around the tank to prevent shadows from being created, as so the observer could observe the fish through a viewing hole so as not to disturb the fish (Fig 3).

Statistical Analysis: Statistical analysis was done using t-tests for comparisons between sex with parameters of boldness and exploratory behavior. Size, boldness and sex were compared with an ANCOVA. Boldness measures would be based on how long it took for the guppy to leave the initial refuge site. If the guppy leaves the refuge for more than 10 seconds, it counts as leaving the initial site. Exploration behavior was measured after 5 minutes of leaving the initial refuge site. The maximum time allowed for a fish to leave the refuge was 45 minutes or 2700 seconds. The reciprocal of time to emerge is considered to be a measure of boldness, and amount of area covered after leaving the refuge is called exploratory tendency, or at least, activity.

Predator Trials

For the predation study, a prawn, *Macrobrachium spp.* was placed at the other side of a tank with a glass partition between the guppy and the predator. The predator was chosen based on previous studies of guppies interacting with prawns in the wild (McKellar et al 2008). Then using the same pvc piping initial refuge, the boldness of individuals were measured using the same methods as the initial boldness and exploratory behavior study. The tank was smaller in size 45cmx43cmx23cm and water was filled up to 4cm within the tank. The pvc piping refuge was used and the fish were allowed to acclimate for 10 minutes within the enclosure. 15 male guppies and 15 female guppies were tested for this study. This study involved a control and compared guppies, male vs. female.

3 kinds of trials were held per fish visual, chemical and a combination of visual and chemical.

1) The predator was placed with a partition (Visual only)-using a glass partition between the predator and prey
2) Only water that the predator has been in (chemical only) was poured into the tank with the guppy.
3) The predator on the other side of the tank along with the water from which the predator was inside was placed in the tank with the guppy. (visual and chemical)

Statistical Analysis: Statistical analysis was performed using R. The means were compared using the Wilcoxon rank sum test and a post-hoc pairwise comparison Kruskal-Wallis rank sum test.

FIG. 3 Behavior apparatus with tank, 4x4cm grid, pvc pipe refuge, camera and curtain

Survey of Guppies

The guppies were surveyed by fish count of 150m of the Opunohu watershed. The sites were: S 17°31.543′, W 149°50.199′ (100m) and S 17°31.536′, W 149°50.003 (50m) and 150m of the Pao Pao watershed: S 17°30.877′, W 149°49.419′ (100m) and S 17°30.925′, W 149°49.911′ (50m). Each pool and riffle was examined for guppies and I remained at each pool and riffle I came across walking along the stretch of 100m or 50m. I would stop at each pool and riffle for 10 minutes and observe all sides of the pool or riffle and then continue.

RESULTS

Boldness and Exploratory Behavior and Sex

A total of 28 trials were conducted. There were 15 female trials and 13 male trials. (Fig 4 above). Boldness measures were made by taking the reciprocal of the time it took for males and females to come out of the refuge and into the novel environment. Males were significantly more bold than females. (T.test p=0.02) The mean of the female trials was 0.01 and the standard deviation was 0.02. The range of 2700 seconds given for each trial, two of the females took the maximum time and did not leave the refuge for 45 minutes. For males, the mean was much greater, 0.13 and the standard deviation was 0.2. There were three males that took the least amount of time to leave the refuge, 2 seconds. Two of the male trials were not considered because there was not enough time for the trials to reach completion.

The exploration tendency, (Fig. 4 below) was quantified by counting the number of 4cm x 4cm squares that the fish covered after 10 seconds of leaving the refuge. The video was analyzed for 5 minutes. There was little difference between the amount of area covered for males and for females. The significance value was (T.test p=0.30) which was not significant. The mean value for females was 1070.9 cm^2 and 1038 cm^2 for males. The standard deviation was 894.5 for females and 596 for males.

Boldness and Exploratory Behavior and Size

Size and boldness was taken into consideration using sex as a grouping factor (Fig 5) for an ANCOVA using R. This shows there is no relationship between size and

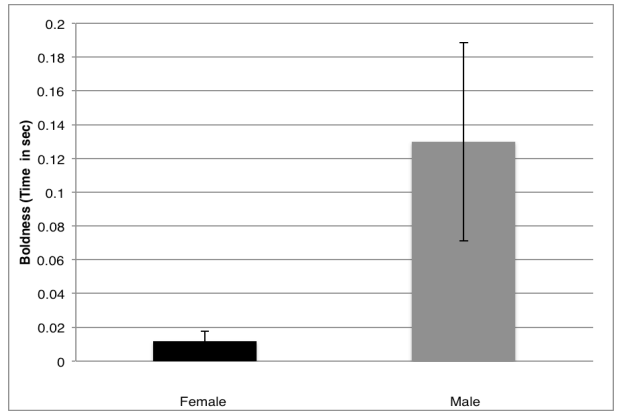
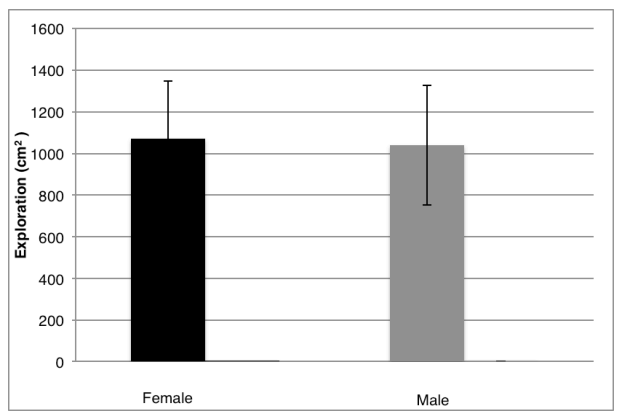


FIG. 4 Boldness of males and females (above) and Exploratory behavior of males and females. (below) Significance in boldness between males and females (p=0.02) and no significance in exploration tendency (p=0.30)



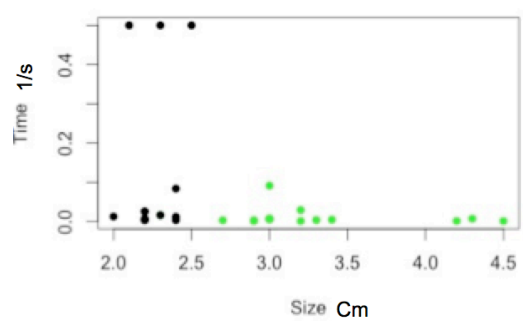


FIG. 5 Boldness-Time (1/sec) and Size (cm) ANCOVA
Black=male and green=female

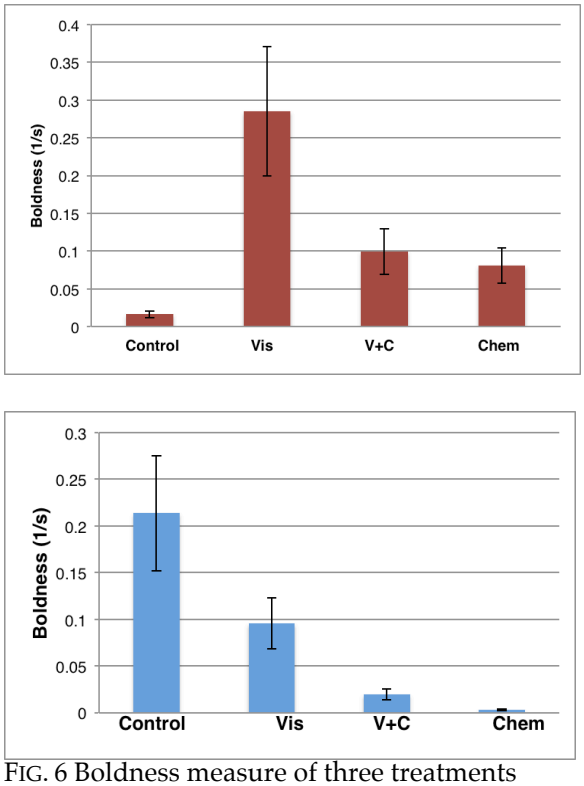


FIG. 6 Boldness measure of three treatments (vis-visual, V+C-visual and chemical, Chem-chemical)
plus the control. Females are above and Males are below. Wilcoxon rank sum test p=0.10 Kruskal-Wallis rank sum test, p=0.029

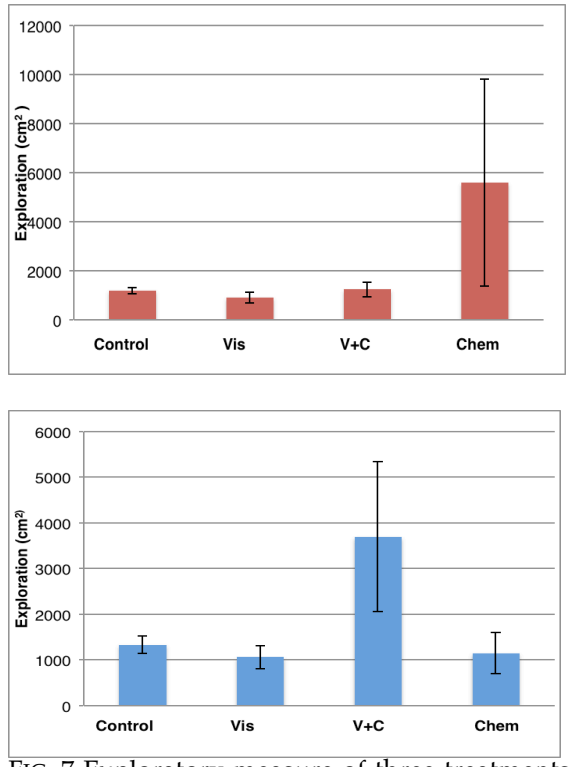


FIG. 7 Exploratory measure of three treatments (vis-visual, V+C-visual and chemical, Chem-chemical) plus the control.
Females are above and Males are below.
Kruskal-Wallis rank sum test p=0.5

boldness. However, there is a pattern showing the sexual dimorphism between the males and females. Males also had higher variation in their latency times, indicating three bold individuals with 0.5 1/s values.

Predator Trials

In comparisons for boldness of predator trials, 3 treatments involving visual cues, chemical cues, both visual and chemical cues, as well as a control revealed there was a significant difference between the different treatments for males and females. (Kruskal-Wallis rank sum test. P=0.029) For the post-hoc test a pairwise Wilcoxon rank sum test was used (p=0.10). The control for males and the visual trials for males had significance (p=0.014) as well as control for males and chemical trials for males. (p=0.019) Females had differences between the visual and visual and chemical trials. (p=0.014) There was also a difference between the control trials for females and the visual trials of the males. (p=0.04). There were 24 control trials, 23 visual trials, 23 chemical trials and 23 both cue trials. (Fig 6) Female boldness seemed to increase in the presence of visual and visual and chemical cues while males had a decrease in boldness for visual and chemical trials in comparison to their control.

The means for female control, visual, V+C, and chemical trials were 0.02, 0.28, 0.1, 0.08 (1/s) respectively. The means for the male control, visual, V+C, and chemical trials were 0.2, 0.09, 0.012, 0.003 (1/s) respectively. Exploratory behavior of male and female guppies did not differ significantly (Fig 7). (Kruskal-Wallis rank sum test p= 0.5) Although there were slight increases in the chemical trials for females and for the visual and chemical trials for males, there was no significance. The mean of the female trials for control, visual, visual and chemical, and chemical cues were 1201, 909, 1230, and 5590 cm^2 respectively. The mean of the male trials for control, visual, visual and chemical, and chemical cues were 1333, 1062, 3693, and 1149 cm^2 respectively as well. For the recorded

trials, there were 22 control trials, 20 visual trials, 23 chemical and 21 both cue trials.

Survey Results

I observed that the guppies preferred areas with deep pool, and low water flow. Often, there would be weeds or vegetation nearby the bank of the stream where the guppies would talk refuge. When startled, they quickly swam away and hid. On days when it rained or was raining it was difficult to see the guppies.

At Pao Pao site 1, I recorded seeing 73 guppies, in a 50m stretch. At Pao Pao site 2, I recorded seeing 113 guppies in a 100m stretch. At the Opunohu site 3, I saw 31 guppies and at Opunohu site 4, I saw 10 guppies. However, it should be noted that at site 4 there was low visibility due to timing of the survey, 5:00pm when the sun was setting.

DISCUSSION

Boldness and Exploratory Behavior

The results of this study have shown that males were bolder than females. Previous studies have also shown this trend (Cote et al 2011). This pattern suggests that sex may have a key role in the behavioral acts of *Poecilia reticulata*. Males are smaller in size, and it is usually assumed that smaller fish are more shy, however, smaller sized fish have faster metabolisms. This may drive the smaller fish to feed more voraciously in comparison to larger fish. In addition, *Poecilia reticulata* are a live-bearing species. They have polygamous mating systems resulting in males needing to be aggressive in order to maximize the number of females they can mate with. While female guppies are only receptive once a month, male guppies are constantly engaging in sexual behavior (Plath et al 2007). The cost of being more bold and aggressive in order to have a chance to mate may outweigh the cost of possibly being eaten, for example. Females on the other hand, are larger and were more likely to stay within the refuge. There were 2 individuals who did not leave the refuge after 2700s. Females perhaps have an advantage to be more cautious. They are wary of males that want to mate. Females also have the cost of bearing and therefore, to protect the next generation of guppies, it may be more beneficial to be more cautious in a novel environment as well. Females are also known not to feed as much in the presence of males, also indicating the costly nature of not being as cautious because males sometimes indulge in a sneaking behavior in the female's blind spot in order to copulate (Plath 1997). Because the apparatus was set up so that the fish would emerge from a familiar, small and dark refuge into a larger, brighter spaces issues of becoming visible and entering a new space are involved in the behaviors of the fish.

Furthermore, there are intraspecific variations in the flexibility that individuals possess when facing novel circumstances. Guppies have been found to have various innovative ability, or ability to adapt, based on sex, size and food deprivation (Wright et al 2010). Males were found to have a correlation between competitive ability and innovative ability but not females (Laland and Reader 1999). Perhaps males are able to adapt to new situation more easily than females.

There are other factors that could be considered in regard to the behavior of male guppies and female guppies. Hormones that are often linked with the phenotypic behaviors may also be indicators of the variation seen within groups and between sexes. Male aggression such as male-male competition is linked with hormone levels. A recent study had found that the presence of the pesticide atrazine, reduced aggression in males and dulled signal sensory, resulting in loss of female interest and receptive behavior (Shenoy 2012). Males are also known to prefer cooler temperature water compared to females which may have been a possible confounding factor of the study since water temperature was not considered.

In a previous study, by Cote in 2011, there was a positive correlation found between boldness, exploratory behavior and dispersal. They also found that there was no relationship between body size, or mass, and the exploration activity of males and females. Similarly, exploration activity was found to be similar in all the trials including the predator trials of this study. This may indicate the innate qualities that the guppies in Moorea possess, make them a stable and established population. In order to move from the stage of spreading to the stage of establishment in the process of invasion, dispersal ability should be key. Therefore, this result relates the invasive ability of the *Poecilia reticulata* population within Moorea. Even though there may not be a significant difference between the two sexes, males were slightly greater in their area covered in comparison to females. Males were also seen to forage and vary in the depth of

water while swimming during trials, which may relate to their exploration and boldness behaviors. The behavioral state of the guppies during trials, could also have been influenced by their levels of starvation. Female guppies were often by the darker shaded regions of the tank behind the refuge and often swam sporadically.

Size and boldness were found not to have a significant correlation however, it should be noted that there was higher variability within the group of males. Females are seen to have more of a consistent time of latency in comparison to males. The result also showed the sexual dimorphism between the two species. Three of the males were particularly bold, only taking 2s to leave the refuge. Their sizes varied and they all had similar colorations perhaps it was because of confounding factors that they left the refuge quickly since I had put the males and females together in the same container in between trials. These males may have also been innately aggressive, although further experimentation would be needed to prove that.

Predator Trials

With the predation trials, there did not seem to be a clear pattern between males and females. Within their sexes however, there was a clearer distinction in reactions to the presence of a predator. A previous study had found that changes in behavior due to predators, might result in more cautious behavior such as less foraging and exploration (Rehage et al 2004). Males were less bold in the presence of a predator with visual and chemical cues. This shows that males are sensitive to these cues, which are also important for mating. Chemical cues from females like estrogen and pheromones and visual cues of spotting a female are important adaptations (Shenoy 2012). Also due to the coloration of male guppies, it may be more beneficial for them to be more cautious and less bold in the presence of a predator outweighing the benefit of mating. Guppies that are surrounded by predators often do not display vivid coloration compared to other less predated guppy populations (Reznick et al 2001). Females on the other hand, were found to have bolder trials during the visual and visual and chemical trials. These cue reactions may also indicate traits that female guppies are more receptive to. Because of the nature of their mating system, female guppies mainly focus on visual cues in order to spot and sometimes avoid males (Plath et al 2007). In reaction to a predator, possessing a bolder behavior also correlates with the finding that fish may not necessarily act with more caution in response to a new predator (Magurran and Seghers 1990). Females have also been known to participate more in anti-predator behavior and initiate the investigation of a predator when other fish are present as well (Magurran et al 1991).

These findings give an insight on the correlations between invasiveness, boldness, and exploratory behavior of the guppy, *Poecilia reticulata*. Their characteristics within the context of encountering a novel environment and predator are important in understanding the stages of invasion and the adaptation or innate traits, which made this species successful. Their impacts and role on the community structure in the island of Moorea should be further investigated.

Survey

Guppies are in both the Opunohu watershed and the Pao Pao watershed. There may be other watersheds and streams where they have spread across Moorea. They are small and so sampling is optimally done in observing and capturing with smaller nets and not with a seine net. There were more guppies in the Pao Pao watershed compared to the Opunohu watershed, although the range of the survey (150m) is a small portion of the stream. The habitat preferences of the species could be looked into more in-depth. I had observed a preference for deeper, calmer water often with refuges of tree trunks or weeds available. They were also seen to be eating algae and were larger in size by the Pineapple plantation and Are's market suggesting that the Pao Pao watershed may have eutrophication or more nutrients. The Opunohu watershed sites were slightly further from agricultural areas and had less man made habitat alterations.

Possible directions in the future would be to include the variable of predator size and how it affects the boldness and exploratory behavior. In addition, testing whether there is a difference in boldness and exploratory behavior between native fish and invasive fish within Moorea could be an insightful study, preferably a fish that competes with the guppy and lives in the same habitat niche, living in the water column. The expanse of the invasive guppy should also be investigated since a preliminary survey was made. There could also be studies on the differences in shoaling and foraging behaviors fish in Moorea possess.

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APPENDIX A

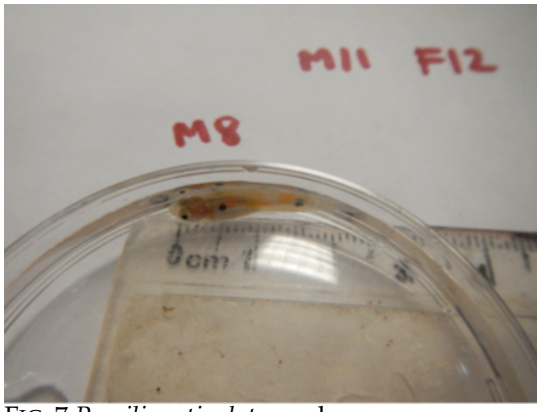


FIG. 7 *Poecilia reticulata*, male

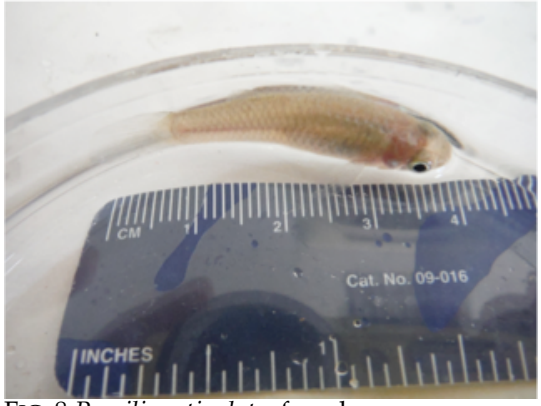


FIG. 8 *Poecilia reticulata*, female

FIG. 9 *Macrbrachium spp.*, male

FIG. 10 Chart of female guppies and size

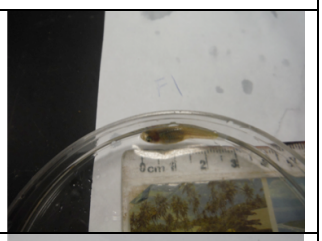
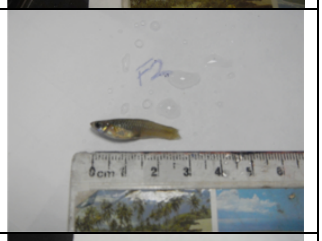
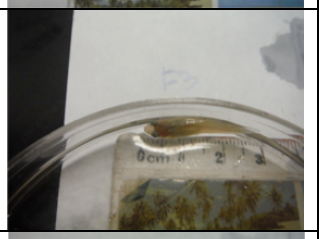
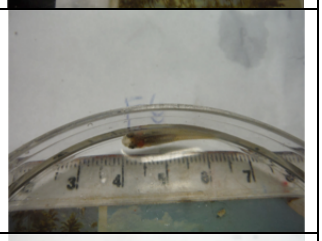
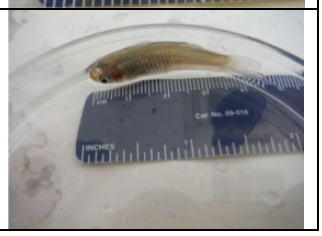
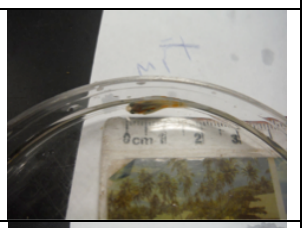
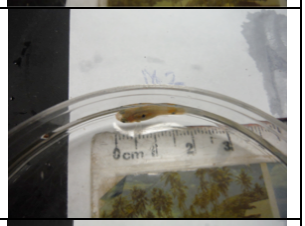
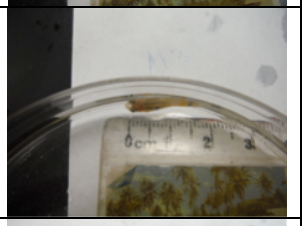
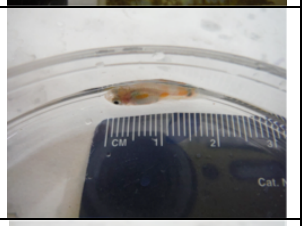
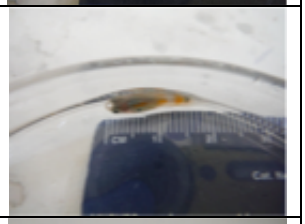
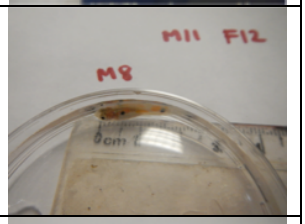
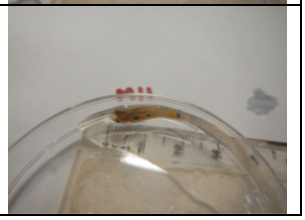
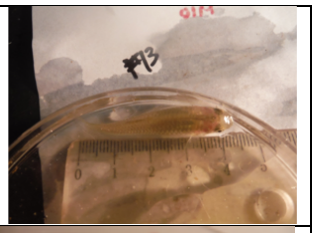
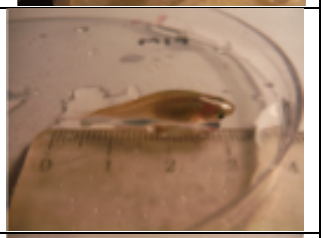
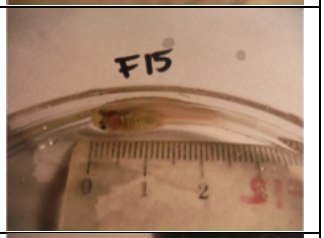
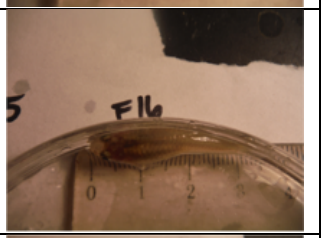
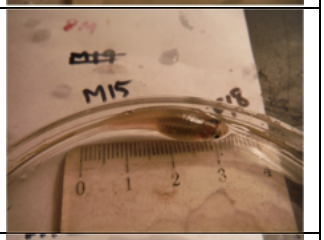
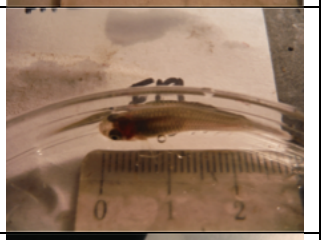
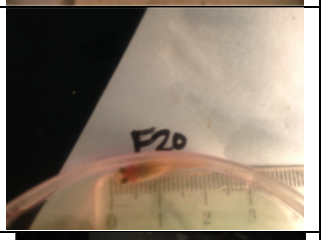
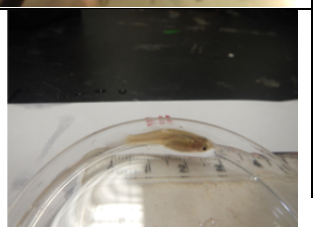
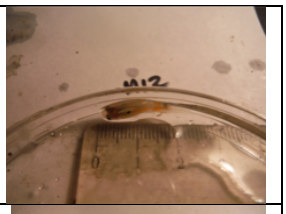
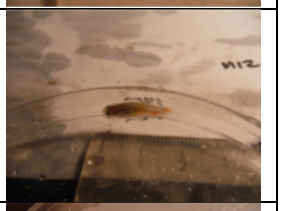
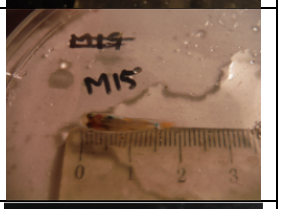
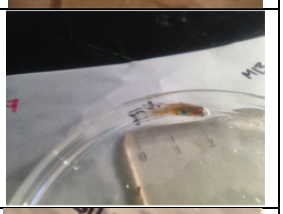
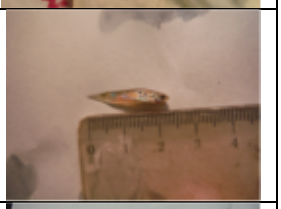
Guppy	Size (cm)	Picture
Female 1	3.2	
Female 2	2.9	
Female 4	3	
Female 6	2.7	
Female 7	4.2	
Female 8	4.5	

FIG. 11 Chart of male guppies and size

Guppy	Size (cm)	Picture
male 1	2.3	
male 2	2.4	
male 3	2.3	
male 6	2.2	
male 7	2.2	
male 8	2.1	
male 11	2.5	

Female 13	4.3	
Female 14	3.2	
Female 15	3	
Female 16	3.4	
Female 18	3.3	
Female 19	2.9	
Female 20	2.3	
Female 11	3	

male 12	2.4	
male 13	2.2	
male 14	2.2	
male 15	2	
male 16	2.4	
male 17	2.1	
male 20	2.4	
male 4	2.2