DOMINANCE DISCOVERY TRADEOFF OBSERVED IN INVASIVE ANT SPECIES *S. GEMINATA* AND *P. LONGICORNIS*

MICHELLE A. HERSHEY

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

Abstract. By using baiting experiments I was able to determine the existence of a dominance-discovery tradeoff among invasive species of ants *S. geminata* and *P. longicornis.* The structure of communities of invasive ants are important to understand and map out in order to structure the most efficient way of preserving biodiversity. There were six species of ants chosen as the subject of this study *Pheidole megacephala, Monomorium floricola, Tetramorium sp, Tapinoma melanocephala, S. geminata* and *P. longicornis.* Due to relative abundance of *S. geminata* and *P. longicornis* these two species were chosen to model the existence of a dominance-discovery tradeoff. By measuring differences in discovery ability I was able to find that some ants were better at discovering food sources than others. *P. longicornis* was often first on baits and showed superior discovery ability. By contrasting the differences in recruitment rates I was able to determine dominance. *S. geminata* was on average the more dominant species on baits where both species were present. By comparing and contrasting these two species in trials where both were present, I found that *S.geminata* adopted the role of "extirpator" and *P. longicornis* fit the role of "opportunist" within this tradeoff.

Key words: Invasive ants; community structure; Discovery Dominance, Marquesas, French Polynesia; Invasive community structure , Tradeoff

INTRODUCTION

In order to predict the patterns of disturbance and prevent the spread of disturbance caused by an introduced species, it is important to first understand the mechanisms that contribute to the success of invasive species (Feener 2008). Invasive species are able to fill and even create niches that didn't exist previously(Bernstein et al. 1979). A key step in determining these mechanisms is determining the interactions among invasive species at a community level rather than just a species by itself. Invasive ants have been reported to coexist as invasive communities worldwide (Morrison 1996, Perfecto and Vandermeer 2011, Holoway 1999, Bernstein and Gobbel 1979) and the behaviors of each species and the role each play in invasions may change depending on what other species are present. So it is imperative to consider these relations among species and determine what is known in order to step back and approach the problem of invasive species from a more holistic standpoint. This study aims to reveal more about the interactions among invasive ant species and specifically to determine the existence of the dominance-discovery tradeoff between invasive species *Pheidole megacephala, Monomorium floricola, Tetramorium sp, Tapinoma melanocephala, S. geminata* and *P. longicornis.*

According to the principle of competitive exclusion described by Gause, coexisting species can't exceed a certain "limiting similarity"(Gause1932). If two spatially overlapping species are contending for the same resource, natural selection would cause one to dominate over the other resulting in the exclusion or extinction of one species from the habitat (Holloway 1999, Levings et al. 1981). Alternatively, the competition over the same resource could result in the formation of new niches, which would lead to evolutionary changes that would minimize competition. Specialization of foraging behavior is a way to form new niches in a way that would decrease interspecific competition (Wilson1971)

These four main invasive ants share a similar omnivorous diet (Wetterer 2003) yet are able to coexist in the same range (Shirley 1999, Morrison 1996). One explanation for this coexistence could be explained by the dominance-discovery tradeoff. Davidson (1998) describes the dominance-discovery tradeoff in a paper categorizing three different foraging strategies—"opportunists" are often first to find the baits but tend to retreat when faced with interspecific competition. "Extirpators" compensate for their slower discovery time by recruiting in larger numbers more quickly than the opportunists and ousting other species more aggressively.

Lastly, "insinuators" typically forage discreetly while other ants are present on the bait but are generally not disturbed because of their smaller size and inconspicuous behavior (Wilson 1971).

This experiment will look at *Pheidole megacephala, Monomorium floricola, Tetramorium sp, Tapinoma melanocephala, S. geminata* and *P. longicornis* and will measure interactions among these different invasive species noting factors such as discovery time and dominance to determine if there is a dominance-discovery tradeoff present. This behavior is not applicable if the six species are able to coexist due to differences in dietary preferences between protein and carbohydrates. These ants are known to share a similarly generalist diet and I hypothesize this fragmentation of the community is therefore due to a difference in foraging strategies (Bernstein 1979) After testing for differences in dietary preferences, I will continue to investigate the possibility of a dominance-discovery tradeoff. The next step is measuring discovery time and quantifying dominance of a food source.

This study consists of four parts: (1) Composition of the community is an important factor to consider when studying behavioral traits, as behaviors may change depending on the individual species that are in contact with one another. I will determine the composition of the community at each of the four sites I performed experiments at. (2) I will be determining dietary preference in order to reject the hypothesis that the breakdown in the community is due to different nutrient preferences. In order to test for the presence of a dominance-discovery tradeoff I will (3) measure discovery times. I hypothesize that there will be distinct observable behavioral qualities that show some ants to play the role of "opportunists" dictated by difference in discovery time among invasive ant species. (4) I will quantify and determine the dominance of a food source. I hypothesize certain species of ants will exhibit the behavior of "extirpators" and certain species will be more dominant than others. This dominance-discovery tradeoff has been observed in many parts of the world(Feener 2008) . I think this tradeoff offers an explanation for the coexistence of these multiple species of invasive ants observed on Mo'orea, French Polynesia. My findings will contribute to the existing knowledge of the invasive ant communities on the Society Islands and will help make further deductions on how to best control the spread of these invasive ants.

This study focused mainly on interactions between *S. geminata* and *P.longicornis* due to their relative abundance on the island. However, data was collected and analyzed on all six of the previously mentioned species.

METHODS

Studies were conducted at four study sites in order to ensure that the behaviors of all the species were observable across multiple geographic regions. Testing at different sites removed the possibility of the behaviors being tied to specific environmental factors and that the prevalence of a dominance-discovery tradeoff was not only restricted to one locality. These four sites were the Public Beach (17°29'29.09"S 149°51'1.74"W) the UCB Gump station (17°29'26.43"S 149°49'35.80"W) the Belvedere (17°32'25.37"S 149°49'36.68"W) and the Lycee Agricultural School (17°31'58.67"S 149°50'0.17"W).

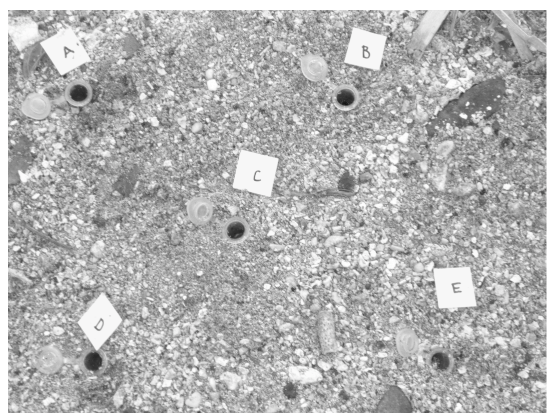

Figure 1: Experimental set up for trials testing both dominance and discovery. Five 1 mL vials placed within a 15cm quadrat each containing a solution of 40:60 sugar:water solution.

Dietary Preference

A baiting experiment was performed to determine if different ant species showed a similar preference for sugar and protein. Twenty pairs of 1mL plastic vials were placed in a 10m diameter ring around the Public Beach.Twenty of the baits were filled with a

40:60 sugar to water solution. The other twenty were filled with an extraction of water drained from a can. The different baits were placed in pairs side by side and were observed every minute to record for the presence or absence of *Pheidole megacephala, Monomorium floricola, Tetramorium sp, Tapinoma melanocephala S. geminata* and *P. longicornis* .

Testing Discovery

Within the context of the dominance-discovery tradeoff, discovery of a species must be measured directly against the discovery ability of another species. Superior discovery ability was quantified and averaged across all species by dermining how long it took for each ant species to find baits starting from the moment each bait was put out. I began timing immediately after the last vial was filled with the sugar solution. Once a bait was reached by a species, the time taken to reach the bait was recorded. Additionally the identity and order of arrival was recorded for up to three species. Ants were later removed with an aspirator and identified under a microscope.

Testing dominance

Trials testing for dominance were set up to test recruitment abilities rather than superior fighting ability. In order for one species to be more dominant than the other, this species must have a faster recruitment rate. To determine which species had the faster recruitment rate, the differences in recruitment rate from the beginning to end of a specified time period were compared against each other. Rates were graphed using JMP 9.0 and a line was added to track the change in rates from beginning to end. The more dominant species was the one whose line had a steeper slope. The ant that shows the steeper slope is the ant that was able to increase its recruitment rate to a higher number over the same time interval. Trials to test for dominance were set up in the same manner as the tests for discovery (Fig. 1.) Trials lasted for thirty minutes. I recorded the species and number of ants present on each bait (N) in 3 minute time intervals. From these numbers I was able to generate a graph of the change in rates of ants at each time interval (Eq. 2.) and then ultimately graph the average change in rate from beginning to end of the trial (Eq. 3.).

$$r_i = \frac{\Delta N_i}{3(\text{min})}$$

Eq. 2. Change in rate is determined by looking at the change in number of ants over each three minute time interval.

$$D = \frac{r_f - r_i}{\Delta t}$$

Eq. 3. Dominance is determined by calculating the change in rate from the first time interval where both species are present until the end of the trial. Whichever species has a larger D value is the species that is considered to be more dominant.

Additionally, graphs generated using MatLab were created to show the average trends in number and rate over time of the two species in question.

Statistical Analysis

All statistical analysis was done using JMP version 9.0.0 and all maps depicting presence of various species of invasive ants within an invasive community were produced with Google Earth Pro.

Dietary Preference

A chi-square analysis was used to test *S. geminata* and P. *longicornis* preference for protein or carbohydrate based food items and to determine if there were any trends or significant deviations from the null hypothesis that all ants prefer both food types equally. I hypothesized both species would choose protein baits half of the time and carbohydrate baits the other half of the time.

Modeling Discovery

One-way analysis of variance (ANOVA) and Tukey-Kramer tests were used to measure differences between different discovery times of all species *Pheidole megacephala, Monomorium floricola, Tetramorium sp, Tapinoma melanocephala, S. geminata* and *P. longicornis* recorded over all sites.

Modeling the Dominance-Discovery Tradeoff

Only trials where the two species in question were present at the bait were used in modeling the dominance discovery tradeoff. A

Chi-square analysis was used to test if *S. geminata* and *P. longicornis* to determine if there were any deviations from the null hypothesis that all ants are equally good at dominating and discovering a food source.

Additionally, graphs generated using MatLab were created to show the average trends in number and rate over time of the two species in question.

RESULTS

Out of 250 baits that were put out some baits 167 were discovered by more than one species. There were 264 instances of discovery that occurred by all measured ant species. The frequency of each species was calculated and represented below (Fig. 1.) in percentages of baits discovered by a certain species.

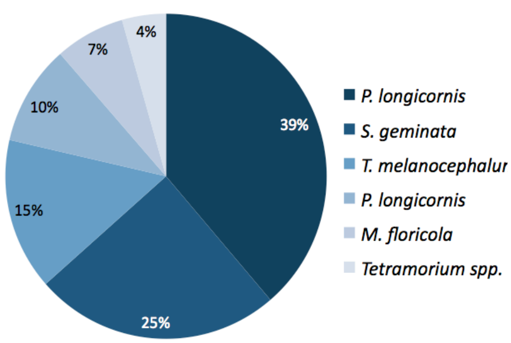

Fig. 1. Percentages of baits discovered by a certain species. Percentages are calculated out of a total of the 264 instances of discovery that occurred by all measured ant species.

Measuring Dietary preference

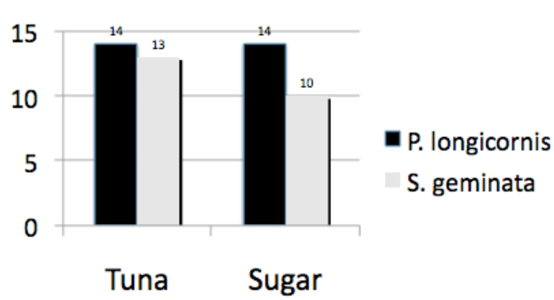

Fig. 2. No preference of protein over carbohydrate has been shown by either *P. longicornis* or *S. geminata*. (Likelihood Ratio, ChiSquare value=.216, P value=0.642)

There were no differences in preference of protein over carbohydrate in *P. longicornis* and *S. geminata*(Fig.2.). Out of a total of 40 baits set out, 39 were discovered.

In this study I am focusing on *S. geminata* and *P. longicornis* , which were observed a total of 172 times. Modeling the dominance-discovery tradeoff requires that both species in question are observed at the bait within the same timespan. This only occurred 27 times, however. There is a significant difference in order of appearance of particular ant species at the baits.

Measuring Discovery

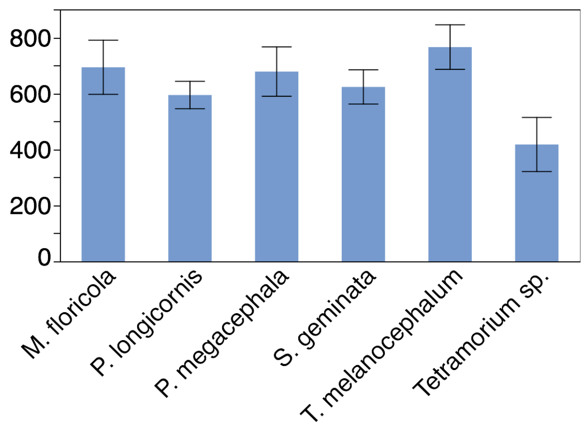

FIG. 3. No significant differences in discovery time among the 6 recorded species of ants. (*M. floricola, P. longicornis, P. megacephala, S. geminata, T. melanocephalum*, and *Tetramorum spp.*).Error bars are present to represent +/- one standard error. (ANOVA, $F_{2,3}$=1.12, P=0.3474)

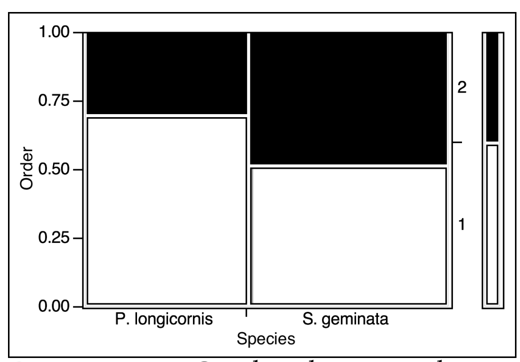

Figure 4. Graph showing the significant differences in order of appearance on 27 baits . *P. longicornis* is often first to find the baits and *S. geminata* discovers the baits second (Likelihood Ratio, ChiSquare value=5.493, P value=.0161)

Out of the 250 baits placed out only 167 were discovered. However, there were 264 instances of discovery by different species across all baits. These 264 discovery times were averaged and sorted by species. No significant difference in discovery ability is shown.

Measuring Dominance

Overall, there are a few species who have significantly different recruitment rates. When average rates are tabulated across all trials and sorted based on species there is no significant difference between *P. longicornis* and *S. geminata.* However, many other species are shown to have a significant difference in recruitment ability (Fig. 5.)

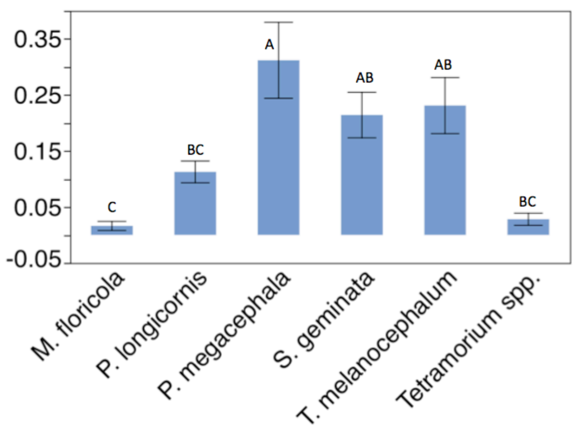

Fig. 5. The average rate of recruitment of each species *(M. floricola, P. longicornis, P. megacephala, S. geminata, T. melanocephalum,* and *Tetramorum spp.*).Error bars are present to represent +/- one standard error. Bars with different groupings of (were found to be significantly different (ANOVA with Tukey-Kramer HSD) whereas bars that share a letter are not significantly different

Because the focus of this study is on the tradeoff between *S. geminata* and *P. longicornis* it is more valuable to measure the difference in recruitment rates of each species only in instances where they interacted with each other. When average rates were calculated for these select trials (Fig. 6.) , I found that *S. geminata* had a higher recruitment rate than *P. longicornis.*

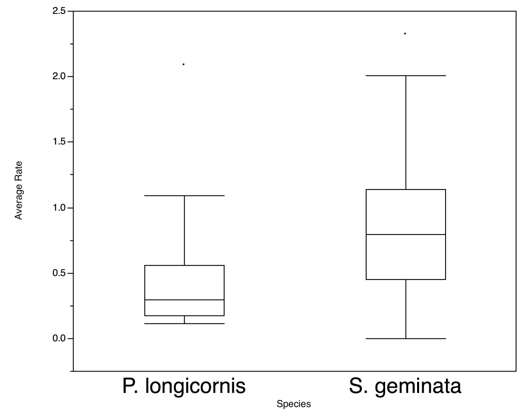

Fig 6. Difference in recruitment rates of *S. geminata* and P. *longicornis* averaged over the 27 trials where both species were present on the bait. (t-test, t_{54}=2.92, P<0.01)

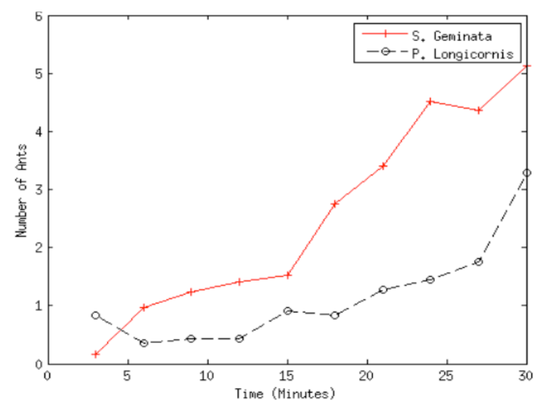

Fig.8. Average number of ants plotted on MatLab over 27 trials where both *S. geminata* and *P. longicornis* were present.

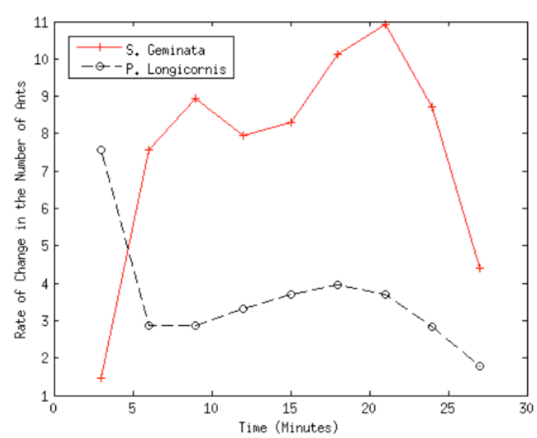

Fig. 9. Average rates of change of *S. geminata* and *P. longicornis* plotted over time.

DISCUSSION

The results of my study demonstrated that there is a dominance-discovery tradeoff observable in *S. geminata* and *P. longicornis.* Because of the relative abundance of *P. longicornis* and *S. geminata* than any other species (Fig. 1) these two species were chosen to model the breakdown of the community of invasive ant species into "opportunists" and "extirpators". This tradeoff has been studied extensively before in the past (Feener 2008, Lebrun et. al 2007, Perfecto, 2011) and it has been shown that competition in ant communities can result in various dominance hierarchies. Although the focus of this study is specifically *S. geminata* and *P. longicornis,* there do appear to be "opportunists" and "extirpators" among other more specific communities (for example at the Agricultural school)(Appendix 1. Fig. 2. .)

Measuring Discovery

There were no significant differences in discovery time among the six recorded species (*M. floricola, P. longicornis, P. megacephala, S. geminata, T. melanocephalum,* and *Tetramorum spp).* (Fig. 3). But this does not necessarily mean that all species have the same ability to discover food. The differences in discovery time were averaged across all species and were represented by a limited sample size. In the future, increasing the number of trials would decrease the inconsistency in discovery time by reducing the variability caused by differences in nest size or distance away from a nest. Also, external factors such as weather, human disturbance, or time of day will play less of a role in affecting these discovery times.

It was more important to look at who was better at discovering (or dominating) when both species were present. When I looked at the differences in order of appearance between *P. longicornis* and *S. geminata* in the 27 trials where both appeared together I found that *P. longicornis* was more often first to appear on the bait (Fig. 4). This would suggest that *P. longicornis* is the "opportunist" within this tradeoff. This role was predominantly observed at the Gump Station and at the Public Beach. However at the Agricultural School other species such as *M. floricola* and *Tetramorium spp* and *T. melanoocephala* were oftentimes able to discover the baits before *P. longicornis.* This suggests that roles of each species within each community vary depending on what other ant species are in the same territory and may also be affected by the composition of the habitat.

Other species such as *M. floricola* and *Tetramorium spp.* have also exhibited relatively better discovery abilities compared to *T. melanocephala* (Appendix 1 Fig. 1,2). So it seems as if there is some transitive hierarchy that can be established based on studying a dominance-discovery tradeoff concerning several communities with overlapping species. But when testing a tradeoff or an interspecific interaction it is necessary to physically confine the two species to a shared space. These instances occurred very rarely among certain species if at all, and limited my ability to construct a hierarchy.

Measuring Dominance

Although not all of the average recruitment rates were statistically different from one another, the datum suggests that there are certain species, which are able to recruit faster than others (Fig. 5). In this study behavioral dominance is the ability of an ant to gain or maintain control of a resource through superior fighting or recruitment abilities (Feener 2008). Previously studies in the Pacific have been done to create hierarchies based on fighting abilities (Morrison 1995). Instances of aggression were noted throughout the experiments, however this study is unique in that it looks at differences in recruitment rates as a determinant of dominance.

On average, *S. geminata* showed a better ability to recruit more ants than did *P. longicornis* and suggests that *S. geminata* adopts the role of the "extirpator" within this tradeoff. *S. geminata* and *P. longicornis* were often seen together at the UCB Gump station, and the Public Beach. Occasionally they were observed at the same bait at the Agricultural school, but this was less common. Interestingly, species at the agricultural school such as *Pheidole megacephala, Monomorium floricola, Tetramorium spp,* and *Tapinoma melanocephala* were showing signs of dividing the community into "opportunists" and "extirpators" (Appendix 1. Fig1,2) where *T. melanocephala* was the extirpator and *M. floricola* and *Tetramorium spp.* were "opportunists". There were not enough instances of *M. floricola* and *Tetramorium spp.* to compare whether or not there would be a dominance discovery tradeoff between those two species. Although average discovery times and average rates have been calculated, this does not replace observing the interactions explicitly between those two species in the field.

P. megacephala is another commonly invasive ant that changing ecosystems worldwide Wilson and Taylor 1967a, Hoffman 1999). In my study, it shows the highest recruitment rate of all ant species identified (Fig. 5) but was never observed enough times with other species to determine whether or not it would outcompete *S. geminata. P. megacephala* is known to outcompete many native and even introduced species of ants (Hoffman 1999). At the Belvedere lookout all of the baits put out were only discovered and dominated by *P. megacehpala.* At the Agricultural school it was seen ousting *T. melanocephalum* from baits after finding them. The inability to produce significant results capturing any comparative differnce of foraging strategy of *P. megacephala* is consistent with past literature that comments on the dramatic reductive effect on the presence of native and introduced species of ants by *P. megacephala* (Hoffman 1999). In future studies, finding the border between the range of *S. geminata* and *P. megacephala* would be beneficial to our understanding of these invasive communities and how dominant species are distributed.

At the Agricultural school there is also a trend of certain ants (*Tetramorium spp.* and *M. floricola*) exhibiting "opportunist" tendencies while *T. melanocephalum* was more of an "extirpator". However, when approached by *P. megacephala* it always retreated from the bait -- a quality of "opportunist" behavior. Again, this shows that different roles can be exhibited by the same species and can be characterized by the surrounding species and environment.

Invasive Ant Communities

This study has shown strong evidence supporting the existence of a dominance-discovery tradeoff between *S. geminata* and *P. longicornis.* Furthermore by looking at the average comparisons of the number and rate of these two species we can see some interesting trends. First, although overall, *P. longicornis* discovered baits more (Fig 4). There is ultimately a greater number of *S. geminata* at the end of the trial (Fig. 8.). By 6 minutes *S. geminata* finds the bait, one time interval after *P. longicornis*. If you look at the change in rate of *P. longicornis* from t=3 to t=6 there is a very sharp decrease in the recruitment rate juxtaposed by a very sharp increase in recruitment rate by *S. geminata*. This ability of a species to be able to recruit more ants is characteristic of "extirpators" foraging strategy. This, paired with field obsevations of aggressive behavior and "chasing away" *P. longicornis* supports my hypothesis that there is a dominance-discovery tradeoff between these two species.

Also, there are observations of other dominance-discovery tradeoffs prevalent among other species (*T. melanocephalum, Tetramorium spp.* and *M. floricola)*. This study was limited by the species (and combinations of species) that appeared on the bait. Increasing the sample size should make constructing a hierarchy or map of interactions of all 6 species less difficult-- as more interactions should arise , as you expand the number and scale of the project. This would be a very beneficial subject for future research.

Because the entire ant fauna of Mo'orea has been introduced relatively recently and is composed of such a diverse array of species from different origins (Wilson et al. 1967) there are new patterns of coevolution that have arisen due to the interactions between ants that have never shared an evolutionary past (Levings 1981, Morrison 1995). These invasive communities are disturbing the ecosystems and could be potentially paving the way for even more invasive species (Green 2011). However the effects of invading species change over time (Strayer 2006). Invasions are complicated and looking at the invasion history of one particular species is just one part of a web of entangled subjects that we need to elucidate to understand the subject of invasions..

This study shows that *T. melanocephalum* is an "opportunist" when matched against *P. megacephala* but is an "extirpator" when paired with *Tetramorium spp.* and *M. floricola.* Just as different species can fill different niches, different niches can be applied to various species. In order to get a better understanding of how these invasive species are affecting native ecosystems, we need to look at interspecific interactions and approach the problem with more knowledge of how invasive communities operate and how composition affects species level behavior.

ACKNOWLEDGMENTS

I thank the UCB Gump station, Frank and Hinano Murphy for their hospitality. I want to acknowledge my professors, Pat Kirch, Jerre Lipps, George Roderick, and Vince Resh for all of their time and support over the course of this semester. My GSI's Jennifer Hofmeister, Virginia Emery and Ekaphan Kraichak for all of their help advising me and working out solutions to problems that I thought were impossible for me to solve by myself. I've learned so much from you and I really appreciate all the time you spent making this class so well run. I'd also like to thank Eric Sebastian de Soto for the countless hours spent helping me sift through endless data points and for his fantastic MatLab skills that allowed me to model what I had been observing all along. Also a thanks goes to Eli Sarnat for answering all of my ant identification questions. This would not have been possible without you. I'd like to thank my friends and family for all the support while I was abroad. I appreciate all the time you spent listening to talk about my ant footage. And lastly, I'd like to say thanks to all of my buddies that came out into the field with me and my 20 new friends that made this class the best experience of my life.

LITERATURE CITED

Andersen, A. N., J. C. Z. Woinarski, and B. D. Hoffmann. 2004. Biogeography of the ant fauna of the Tiwi Islands, in northern Australia's monsoonal tropics. Australian Journal of Zoology **52**:97-110.

Bernstein, R. A. and M. Gobbel. 1979. Partitioning of Space in Communities of Ants. Journal of Animal Ecology **48**:931-942.

Brandon, T. B. 2000. The Trade-off between Thermal Tolerance and Behavioural Dominance in a Subtropical South American Ant Community. Journal of Animal Ecology **69**:998-1009.

Davidson, D. W. 1998. Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off. Ecological Entomology **23**:484-490.

Feener, D. H., Jr., M. R. Orr, K. M. Wackford, J. M. Longo, W. W. Benson, and L. E. Gilbert. 2008. Geographic Variation in Resource Dominance-Discovery in Brazilian Ant Communities. Ecology **89**:1824-1836.

Green, P. T., D. J. O'Dowd, K. L. Abbott, M. Jeffery, K. Retallick, and R. Mac Nally. 2011. Invasional meltdown: Invader-invader mutualism facilitates a secondary invasion. Ecology **92**:1758-1768.

Hoffmann, B. D., A. N. Andersen, and G. J. E. Hill. 1999. Impact of an introduced ant on native rain forest invertebrates: Pheidole megacephala in monsoonal Australia. Oecologia **120**:595-604.

Holway, D. A. 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. Ecology **80**:238-251.

Lebrun, E. G. and D. H. Feener, Jr. 2007. When trade-offs interact: balance of terror enforces dominance discovery trade-off in a local ant assemblage. Journal of Animal Ecology **76**:58-64.

Levings, S. C. and J. F. A. Traniello. 1981. TERRITORIALITY NEST DEPRESSION AND COMMUNITY STRUCTURE IN ANTS. Psyche (Cambridge) **88**:265-320.

Morrison, L. W. 1996. Community organization in a recently assembled fauna: the case of Polynesian ants. Oecologia **107**:243-256.

Pedersen, J. S., M. J. B. Krieger, V. Vogel, T. Giraud, and L. Keller. 2006. Native supercolonies unrelated individuals in the invasive Argentine ant. Evolution **60**:782-791. of unrelated individuals in the invasive Argentine ant. Evolution **60**:782-791.

Perfecto, I. and J. Vandermeer. 2011. Discovery Dominance Tradeoff: the Case of Pheidole Subarmata and Solenopsis Geminata (Hymenoptera: Formicidae) in Neotropical Pastures. Environmental Entomology **40**:999-1006.

Richardson, D. M., J. Carruthers, C. Hui, F. A. C. Impson, J. T. Miller, M. P. Robertson, M. Rouget, J. J. Le Roux, and J. R. U. Wilson. 2011. Human-mediated introductions of Australian acacias - a global experiment in biogeography. Diversity and Distributions **17**:771-787.

Savolainen, R. and K. Vepsäläinen. 1988. A Competition Hierarchy among Boreal Ants: Impact on Resource Partitioning and Community Structure. Oikos **51**:135-155.

Strayer, D. L., V. T. Eviner, J. M. Jeschke, and M. L. Pace. 2006. Understanding the long-term effects of species invasions. Trends in Ecology & Evolution **21**:645-651.

Venette, R. C., D. J. Kriticos, R. D. Magarey, F. H. Koch, R. H. A. Baker, S. P. Worner, N. N. G. Raboteaux, D. W. McKenney, E. J. Dobesberger, D. Yemshanov, P. J. De Barro, W. D. Hutchison, G. Fowler, T. M. Kalaris, and J. Pedlar. 2010. Pest Risk Maps for Invasive Alien Species: A Roadmap for Improvement. Bioscience **60**:349-362.

Wetterer, J. K. and S. D. Porter. 2003. The little fire ant, Wasmannia auropunctata: distribution, impact, and control. Sociobiology **42**:1-41.

Wilson, E. O. and R. W. Taylor. 1967. AN ESTIMATE OF POTENTIAL EVOLUTIONARY INCREASE IN SPECIES DENSITY IN POLYNESIAN ANT FAUNA. Evolution **21**:1

APPENDIX A

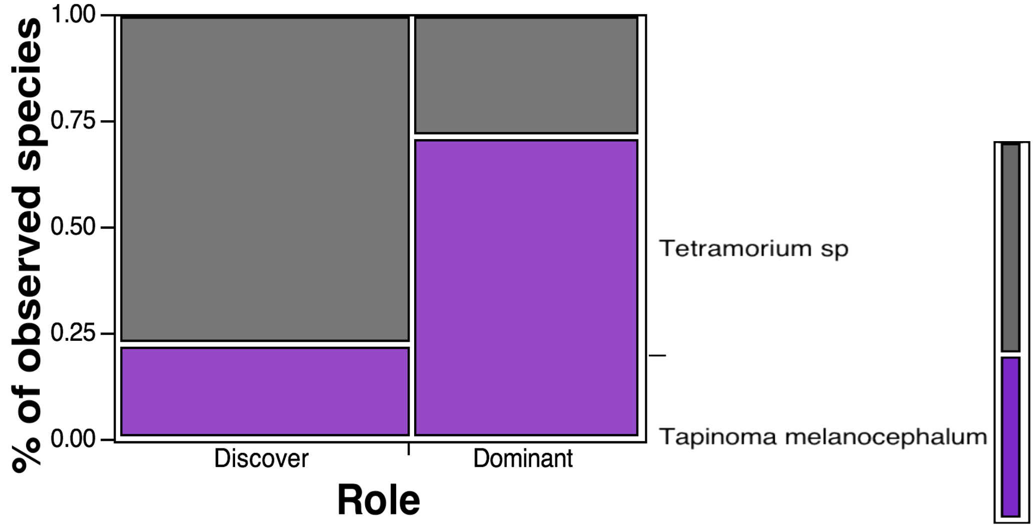

Fig 1. Significant difference in roles of *Tapinoma* and *Tetramorium spp*. Tapinoma discovers in 76% instances observed, TWB dominates in 72.73% instances observed. (Likelihood Ratio, ChiSquare value=4.057, P value=.00440 df=1).

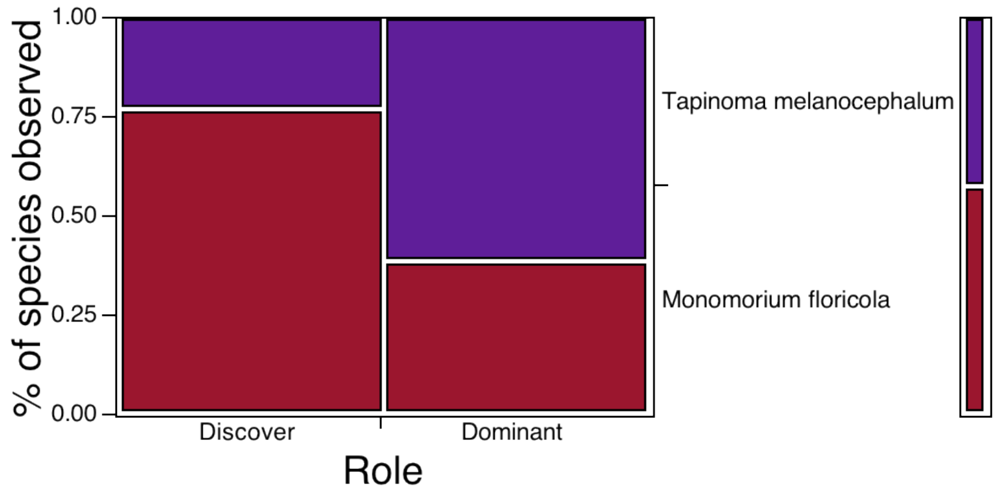

Fig. 2. Significant differences in foraging strategy of *M. floricola* and *T. melanocephalum*. Graph shows more instances of being the first to discover the bait. (Likelihood Ratio, ChiSquare value=4.02, P value=0.0450 df=1).