EFFECTS OF WEB VARIATION ON PREY CAPTURE IN *TANGAROA TAHITIENSIS* (ARANEAE:ULOBORIDAE) SPIDERS AND THE INFLUENCE OF SUSBTRATE, SPIDER SIZE, AND MATERNAL STATE ON WEB CHARACTERISTICS

QI LIEW

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

Abstract. Intraspecific variation in web design has been increasingly recognized as an important aspect of spider ecology and behavior. Why intraspecific variation occurs and how it could affect different individuals' foraging or reproductive strategies remains to be a complex set of interactions which we are still far from fully understanding. In this study, I first show that web variation affects foraging success in *Tangaroa tahitiensis* spiders by using field measurements to demonstrate that number of attachment points and whether the web was exposed or slanted were correlated to prey capture success. In addition, I found that a combination of diameter, number of attachment points and whether the web was exposed best predicted prey capture success. I further show that variability is largely explained by the spider's foraging and reproductive needs, and structural constraints of the substrate did not significantly limit these pursuits. Larger spiders build webs with characteristics which are ideal for prey capture, while mother spiders build webs which are more sheltered. Overall, my findings suggest that although certain web characteristics are better for prey capture, web variation in *T. tahitiensis* spiders persists due to different foraging and reproductive strategies by individuals of different sizes and reproductive states.

Key words: arthropods; Tangaroa tahitiensis; *Uloboridae; orb-web; Mo'orea, French Polynesia; intraspecific variation; predation; foraging strategy; reproduction*

INTRODUCTION

Early predator-prey population models have treated individuals in the same populations as ecologically and behaviorally homogenous (Lomnicki 1988, Kingsland 1995). However, differences among individuals of the same species occur, despite higher genetic similarity within a species than across different species (Lomnicki 1988). Therefore, conclusions about the characteristics of individuals cannot be based purely on observations of entire groups, and vice versa (Martin and Kraemer 1987). Why intraspecific variation occurs and how it could affect different individuals' foraging or reproductive strategies are thus important questions to be asked in order to better understand the ecology and behavior of a species; an important step to take before understanding interactions between species.

Spider webs are easily measured and quantified as products of different resource-use strategies (Blackledge and Gillespie 2004). The main function of a spider web is to detect and capture prey (Shear 1986), but some webs also provide other functions such as reproduction (Shear 1986, Sherman 1994) and protection from predators (Blackledge and Wenzel 2001, Li and Lee 2004). In the past, it was assumed that meaningful variation of the orb-web only existed across different species (Heiling and Herberstein 2000). Recently, more studies have recognized that modifications in web characteristics within a species can affect prey capture (Uetz et al. 1978, Chacon and Eberhard 1980) and spiders may intentionally vary their webs in order to maximize foraging success (Sherman 1994). However, even though certain web characteristics are more advantageous for prey capture, the presence of web variation persists, indicating that there are other factors which may either constrain or affect the web-building of a spider. Such factors include spider size (Eberhard 1971a, Higgins and Buskirk 1992), age (Szlep 1961, Eberhard 1971b, Eberhard 1990), substrate (McReynolds 2000), reproduction (Sherman 1994), previous prey capture success (Sherman 1994), and presence of conspecifics (Gillespie 1987).

Tangaroa tahitiensis (Berland 1934) is a cribellate orb-weaving spider in the family Uloboridae which is native to the Society and Austral islands (Gillespie et al. 2008). Despite being common and widespread along midelevation forests in Mo'orea, French Polynesia, little else is known about the natural history of these spiders. As members of the Uloboridae family, *T. tahitiensis* spiders have no venom (Opell 1979) and therefore they may rely more heavily on their webs to capture and subdue prey. In addition, uloborid spiders produce cribellate silk, as compared to the viscid droplets produced by araneid spiders, and this silk is more costly to produce (Lubin 1986). This coupled with low frequencies of web renewal (Lubin 1986) indicate the importance of constructing a web with the right set of characteristics for an uloborid spider. The range of intraspecific web variation in uloborids is no less than that of the popularly studied araneid spiders, and variation in web characteristics has been recorded in terms of orientation (Lubin 1986), size (Lubin 1986), height (Eberhard 1971a), structure (Szlep 1961, Eberhard 1971b) and stabilimenta (Watanabe 2001). Some studies, such as Watanabe's (2001) study of *Octonoba sybotides*, have linked web variation with prey capture. There are also some studies which show that size or age class of the spider correlate to web design or characteristics. Szlep (1961) found that newly hatched *Uloborus* spiders spin primary type webs that differ in structure from webs produced by the same spider in other life stages. In addition, studies by Eberhard (1971b) showed that "senile" or month old *Uloborus diversus* females spun webs with different structures from other instars, and that there was a positive correlation between size of spiders of the same species and height of web from the ground (Eberhard 1971a). However, few studies have examined intraspecific web variation of uloborid spiders in terms of the trade-offs involved with prey capture and potential physiological or environmental constraints.

The aims of this study are to determine which types and combinations of web characteristics affected foraging success of the relatively unknown *Tangaroa tahitiensis* spiders, and if certain environmental or physiological factors could account for the presence of web variation. I will test the following hypotheses: (1) prey capture success depends on certain types and combinations of web characteristics; (2) dominant substrate, size of spider, and maternal state of spider influences web characteristics. To test these hypotheses, I conducted a large scale assessment of webs in the field. Specifically, I investigated how prey capture success correlates with the following web characteristics which were obviously variable in the field: height of web from the ground, catching spiral diameter, number of attachment points, and whether the web was exposed or slanted. Next, I determined how substrate, size of spider, and maternal state of spider correlated with the above mentioned web characteristics while controlling for the potential confounding effects of the interaction of these factors. I predicted that substrate would cause structural constraints in web characteristics, spiders of different sizes would have different investments in web characteristics due to different energetic needs, and mother spiders would invest more energy in web characteristics that enhance reproductive success instead of prey capture.

METHODS

Study site

T. tahitiensis was surveyed along the 3 Pines Trail in Mo'orea, French Polynesia (17º32'23.55"S, 149º49'33.08"W) from October 2011 to November 2011. The survey began at the start of the trail by the parking lot and the trail at the left fork was taken to loop back to the parking lot. In addition, a survey was conducted on the trail at the right fork until a huge Banyan tree was reached. *T. tahitiensis* spiders were abundant throughout the site and were easily seen from the trail. Preliminary sampling showed that spiders build on several types of substrate in the forest, so only the five most commonly used substrate were used in this study: *Inocarpus fagifer* seedlings, *Angiopteris evecta*, *Syzygium malaccense*, dead branches (woody substrate with no foliage), and *Teratophyllum wilkesianum* ferns.

Web Characteristics and Prey Capture Success

I scanned the vegetation along the trail from ground level to 2m high for *T. tahitiensis*. Even though webs were also found above heights of 2m, I was unable to measure these webs accurately, so they were excluded from sampling. When a spider was discovered on one of the five common substrates, I recorded the following web characteristics: height of web, diameter of catching spiral, number of attachment points, and whether the web was exposed or slanted. I measured the height of the web to the nearest centimeter from ground to the center of the hub of the web. I also measured catching spiral diameter to the nearest half centimeter as the longest diameter of the catching spiral was measured for webs which were not circular. I then counted the number of attachment points (lines from the catching spiral of the web which made contact with the substrate). I considered the web to be exposed if there was no foliage covering the hub of the web, and I considered the web to be slanted if it was estimated to be more than 30 degrees from the horizontal plane. I also puffed cornstarch onto the webs if there was insufficient light to view them properly. I then recorded the presence or absence of prey packages, which were usually spherical or oblong in shape and held in the palps of the spider or left at the hub of the web (personal observation).

In order to determine if certain types of web characteristics correlated with prey capture success, I conducted the following statistical analyses using JMP 9.0.0 (SAS): logistic regression (web height and catching spiral diameter), Pearson's Chi-square test (number of attachment points, whether the web was exposed or slanted). In addition, to determine which combinations of web characteristics were correlated with prey capture success, I ran a fit nominal logistic model with full factorial macros.

Dominant Substrate, Spider Size, and Spider Maternal State and Web Characteristics

I also recorded the dominant substrate the web was built on (substrate with more than 50% of web attachment points; if there were two dominant substrate, the taller one was recorded) and height from the ground to the tallest point of the dominant substrate. Size class of the spider was used as an indirect measure of size and life stage, since it was difficult to measure the length of the spider directly. To verify if what I visually estimate to be large, medium, or small spiders are consistent, I collected spiders from what I believe to be in each of those size classes and analyzed them under a microscope. Lastly, I recorded the presence or absence of egg sacs. Egg sacs were trapezoidal and were often left in a corner of the web (personal observation).

To determine if dominant substrate, spider size, and spider maternal state correlated with web characteristics, I conducted the following statistical analyses using JMP 9.0.0 (SAS): one-way ANOVAs followed by Tukey-Kramer tests (web height and catching spiral diameter), Pearson's Chi-square test (number of attachment points, whether the web was exposed or slanted). In addition, I conducted a one-way ANOVA analysis followed by a Tukey-Kramer test to compare mean heights of substrates to determine if height of substrate was significantly different among each substrate in the same way as web height. To control the effects of potential confounding factors in analyses regarding dominant substrate, I only used large, non-maternal spiders. For analyses regarding spider size, I only used non-maternal spiders on *I. fagifer* seedlings. For analyses regarding spider maternal state, I only used large spiders on *I. fagifer* seedlings. Since I could not differentiate males and females in the field, I was unable to exclude the possible confounding factor of spider gender, although the majority of spiders collected in a preliminary study were female.

RESULTS

Nine hundred webs were sampled in this study. A complete list of the numbers of webs used in each analysis can be found in the Appendix A. Preliminary collection and analyzing of spiders under a microscope show that all large spiders collected were more than 6mm in length. 17 out of 18 large spiders were adults. All medium spiders were between 2mm to 6mm. 14 out of 23 medium spiders were penultimate males or females and 5 out of 23 were likely to be late stage instars. All 22 small spiders collected were less than 2mm and were immature.

TABLE 1. Effects of increasing values of certain web characteristics on prey capture success.

Web Characteristics	Effect on Prey Capture
Height	negative
Diameter	negative*
Attachment Points	positive*
Exposed	positive*
Slanted	positive*

Note: * indicates results which were significant (P<0.05).

Diameter of catching spiral, number of attachment points, and whether the web was exposed or slanted were had significant correlations with prey capture, though height of web did not affect prey capture (Table 1).

Webs with larger diameters had lower rates of prey capture success, although diameter, while statistically significant, is not a good predictor of prey capture (logistic regression, R^2=0.045, P<0.0001). Webs with more attachment points (for webs with 3 to 6 attachment points) had higher prey presence to absence ratios (Pearson's Chi-square Test, χ^2=24.17, df=6, P=0.0005). Exposed webs had better prey capture success (Pearson's Chi-square Test, χ^2=4.37, df=1, P=0.037), and so did slanted webs (Pearson's Chi-square Test, χ^2=30.27, df=1, P<0.0001). Height of web from the ground was not correlated to prey capture (logistic regression, R^2=0.0006, P=0.45).

However, the fit nominal logistic model showed that the best combinations for prey capture success was for webs that had larger diameters, more attachment points, and were exposed (P=0.0056).

Dominant Substrate and Web Characteristics

Substrate type was significantly correlated to height of web from the ground and whether the web was exposed or slanted, but there were no significant correlations between substrate type and catching spiral diameter or number of attachment points. Spiders built webs which were higher from the ground in taller substrates such as *S. malaccense* and *A. evecta* as compared to shorter substrates such as *T. wilkesianum* ferns (one-way ANOVA, $F_{4,257}$=19.70, P<0.0001) and there were significant differences in mean web height between some substrates (Fig. 1).

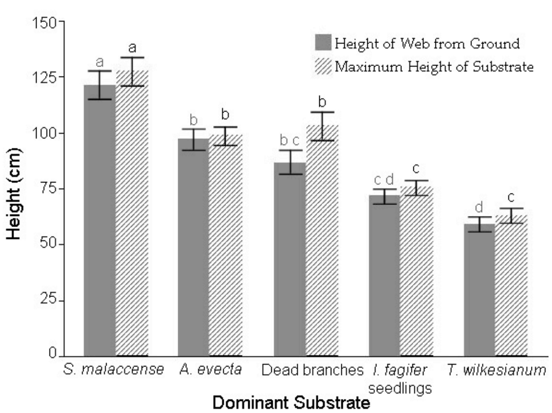

FIG. 1. Mean ± SE height of web from ground and maximum height ± SE of substrate of the five most common substrates *T. tahitiensis* spiders were found on. Different letters above bars indicate significant differences among web and substrate heights of different dominant substrates (Tukey-Kramer Test, P<0.05).

All webs on dead branches and *T. wilkesianum* ferns were exposed, while up to 33% of webs were not exposed in other substrates (Pearson's Chi-square Test, χ^2=30.75, df=4, P<0.0001). A lower proportion of webs on *A. evecta* were slanted than webs on other substrates (Pearson's Chi-square Test, χ^2=9.85, df=4, P=0.043). Substrate type and catching spiral diameter were not significantly correlated (one-way ANOVA, $F_{4,224}$=1.82, P=0.13). There was also no significant correlation between substrate type and number of attachment points (Pearson's Chi-square Test, χ^2=18.24, df=20, P=0.57).

Spider Size and Web Characteristics

Larger spiders built webs that were higher from the ground but there was no significant difference in mean web height between each size class (Fig. 2a). Larger spiders built webs with larger diameters and the mean diameter of each size class is significantly different from each other (Fig. 2b). A higher proportion of large spiders built webs with greater numbers of attachment points (Fig. 2c) and webs that were slanted (Fig. 2e) than smaller spiders. Spider size had no correlation with whether the web was exposed (Fig. 2d). Spider size significantly correlated with height of web from ground, catching spiral diameter, number of attachment points, and slant, but there was no significant correlation between spider size and exposure of web (Table 2).

Spider Maternal State and Web Characteristics

Maternal state of spider was significantly correlated to number of web attachment points and exposure of web, and there was no significant correlation between spider maternal state and height of web, catching spiral diameter, and whether the web was slanted (Table 3). A higher proportion of mother spiders built webs with higher numbers of attachment points than other large spiders on the same substrate (Fig. 3c). In addition, a higher proportion of mother spiders built webs that were not exposed than other large spiders (Fig. 3d). There were no correlations between spider maternal state and height of web (Fig. 3a), catching spiral diameter (Fig. 3b), and whether the web was slanted (Fig. 3e).

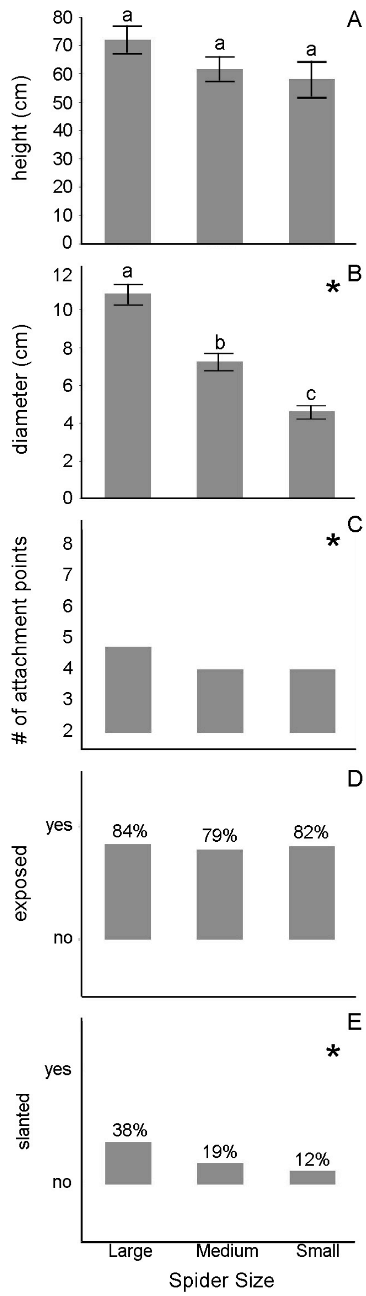

FIG. 2. Height, diameter, number of attachment points, if the web was exposed and if the web was slanted across different spider sizes. * indicate characteristics which were significantly correlated with spider size and where applicable, have significant differences in means. Different letters above bars indicate significant differences among sizes (*P*<0.05), when Tukey-Kramer test was applicable. Error bars represent SE where applicable. For all test statistics and p-values, see Table 2.

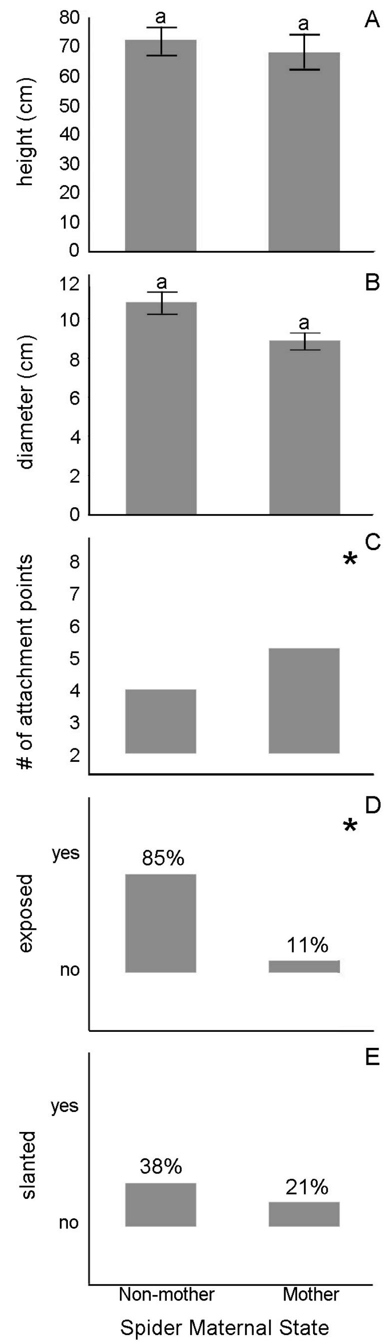

FIG. 3. Height, diameter, number of attachment points, if the web was exposed and if the web was slanted between spiders of different spider maternal states. * indicate characteristics which were significantly correlated with spider size. The same letters above bars indicate insignificant differences among sizes (*P*>0.05), when Tukey-Kramer test was applicable. Error bars represent SE where applicable. For all test statistics and p-values, see Table 3.

DISCUSSION

This study investigates how variations in web characteristics affect prey capture success and explores possible ecological explanations of the persistence of web variation. Results indicate that webs with more attachment points, were exposed or slanted had better prey capture success, and the best combination of web characteristics for prey capture success were exposed webs with large diameters and more attachment points. In addition, dominant substrate could account for variation in height of web from the ground, and certain substrate types could account for whether the web was more likely to be exposed or slanted than webs on other substrates. Larger spiders built webs which had larger catching spiral diameters, more attachment points, and were more likely to be slanted, while mother spiders built webs which had more attachment points and were less exposed. These results show that substrate, spider size, and spider maternal state can influence web variation in *T. tahitiensis* spiders although not necessarily in conjunction with increasing prey capture success. Closer examination of other environmental or physiological factors and web characteristics that I was unable to measure could be useful in order to more fully explain observed web building complexity.

Web Characteristics and Prey Capture

The rate of prey capture success was higher for spiders with webs that had more attachment points or were exposed or slanted. This may indicate the importance of stability in prey capture, given the assumption that webs with more attachment points are more stable. Larger prey are harder to retain in horizontal orb webs (Nentwig 1982). This combined with the lack of venom in all uloborid spiders (Opell 1979) suggests that uloborid spiders may require more time to wrap and immobilize their prey and webs which are more stable could retain prey long enough for the spider to subdue them. The positive relationship between exposed or slanted webs and prey capture could be explained by a higher abundance of prey flying horizontally into webs instead of emerging from the ground or falling onto the web, although this remains to be supported for this system. This could be looked into in the future with the use of sticky traps. Eberhard (1986) found that prey capture success is dependent on flight pattern and angle of incidence of prey impact. Surprisingly, having webs that were higher from the ground did not improve prey capture, despite the findings from most studies that prey capture increases with web height (Brown 1981, McReynolds 2000). The lack of a strong relationship between height of web from ground and prey capture indicates that investment in these characteristics could be due to structural constraints or could be paid off in other ways such as reproduction or

TABLE 2. Statistical test values for correlations between spider size and web characteristics.

Web Characteristics	Type of Test	Test Statistic	p-value	Tukey-Kramer Test
Height	One-way ANOVA	$F_{2,174}=3.13$	0.046	>0.05
Diameter	One-way ANOVA	$F_{2,122}=35.82$	<0.0001*	<0.05
Attachment Points	Pearson's Chi Square	$\chi^2=26.44$, df=12	0.0093*	N/A
Exposed	Pearson's Chi Square	$\chi^2=0.62$, df=2	0.74	N/A
Slanted	Pearson's Chi Square	$\chi^2=9.82$, df=2	0.0074*	N/A

Note: * indicate characteristics which were significantly correlated with spider size and where applicable, have significant differences in means (Tukey-Kramer Test, $P<0.05$).

TABLE 3. Statistical test values for correlations between spider maternal state and web characteristics.

Web Characteristics	Type of Test	Test Statistic	p-value	Tukey-Kramer Test
Height	One-way ANOVA	$F_{1,87}=0.29$	0.59	>0.05
Diameter	One-way ANOVA	$F_{1,65}=3.31$	0.0074	>0.05
Attachment Points	Pearson's Chi Square	$\chi^2=20.40$, df=5	0.0011*	N/A
Exposed	Pearson's Chi Square	$\chi^2=37.70$, df=1	<0.0001*	N/A
Slanted	Pearson's Chi Square	$\chi^2=1.77$, df=1	0.18	N/A

Note: * indicate characteristics which were significantly correlated with spider size and where applicable, have significant differences in means (Tukey-Kramer Test, $P<0.05$).

defense. Alternatively, because I was unable to measure webs which were at heights greater than 2m, I was not able to determine if prey capture differs at heights greater than 2m.

The combination of web characteristics that would best predict prey capture success was diameter of catching spiral, number of attachment points, and whether the web was exposed. Despite showing a weak negative correlation with prey capture, web diameter was important in improving prey capture when it was part of a combination of characteristics. This indicates that larger web diameters were only useful for prey capture if the web was in an exposed location to intercept prey, and if the web had enough attachment points to provide stability to retain captured prey. The result that web diameter only correlated to prey capture when in combination with other web characteristics may explain why previous studies which looked at web diameter as a standalone variable had mixed results. For example, Brown (1981) had reported that webs with larger radii encountered more and larger prey in *Argiope* spiders, but McReynolds and Polis (1987) showed that prey capture rates were not influenced by web diameter in the same species.

Dominant Substrate and Web Characteristics

Webs built on taller substrate such as *A. evecta* and *S. malaccense* were higher from the ground than webs built on shorter substrate; webs built on dead branches and *T. wilkesianum* were always exposed; and webs were less likely to be slanted on *A. evecta*. This suggests that these web characteristics can be constrained by substrate, although overall, substrate had very little impact on limiting web characteristics. The first result shows that *T. tahitiensis* spiders do not maintain a specific range of optimum heights. Instead, spiders build their webs at heights limited by the height of the substrate they are building on. This is consistent with a study done by McReynolds (2000) which also found that mean web height in taller substrates was higher. Secondly, it was expected that webs built on dead branches were always exposed since they were limited by the lack of foliage. Webs built by spiders on *T. wilkesianum* ferns were also always exposed, possibly due to the vertical compaction of fern foliage which does not provide enough space for large spiders to build webs under foliage. Lastly, webs that were built on *A. evecta* were less slanted probably because the structure of *A. evecta* is such that foliage is concentrated on the top of the plant, and therefore spiders will have fewer attachment points at different heights to build slanted webs.

Spider Size and Web Characteristics

Larger spiders built webs that had larger catching spiral diameters, more attachment points, and were more likely to be slanted. Earlier I determined that webs with more attachment points and webs that were slanted were more likely to be successful in prey capture. In addition, exposed webs with larger diameters in conjunction with having more attachment points were best for prey capture. These earlier findings indicate that it is likely that larger spiders build webs with these parameters to enhance prey capture. Larger spiders may have learned from previous experience which types of webs have better prey capture success, and this learning behavior has been shown with Heiling and Herberstein's (1999) work on orb-web asymmetry in *Argiope keyserlingi* and *Larinioides sclopetarius* spiders. Since prey capture did not necessarily improve with increasing web diameter unless in combination with other web characteristics, there should be another reason why larger spiders invest more energy to build webs with larger diameters. In a study by Venner and Casas (2005), increase in web size of *Zygiella x-notata* spiders resulted in an increase in prey capture rates of larger prey. The same study discovered that while large prey are rare, *Zygiella x-notata* spiders require these large but rare prey in order to survive and produce eggs. Therefore, it could be possible that larger *T. tahitiensis* spiders increased their web size in order to capture large prey and gain enough energy to reproduce, although it should be noted that large spiders in my study consisted of both males and females. A possible future direction would then be to measure prey size on top of prey capture success to support this idea.

Spider Maternal State and Web Characteristics

In contrast with other large spiders, I expected mother spiders to divert energy investment away from prey capture to constructing egg sacs and ensuring proper protection for their offspring. Lubin (1986) mentions that egg-sac webs of uloborids are primarily defensive structures. My results show that mother spiders built webs that had more attachment points and were significantly less exposed than normal webs. It is possible that egg sac webs have more attachment points as they may need to be well anchored onto the substrate to prevent wind damage instead of increasing prey capture success. In addition, having a sheltered web instead of an exposed one may prevent predators from easily locating the egg sacs and also shelter the egg sacs from winds and rain. From pictures in a book chapter by Lubin (1986), it appears that other uloborid spiders deposit egg sacs on exposed webs, although other types of spiders such as the theridiid spider *Enoplognatha ovata* place their egg sacs on the undersides of leaves (Seligy 1971). Perhaps risk of predation and damage is higher for egg sacs of *T. tahitiensis* in 3 Pines as compared to other uloborid spiders, which may explain the preference for egg sac webs to be unexposed. Egg parasitoids are common in many tropical uloborid spiders (Opell 1984). However, to my knowledge, no one has studied the wasps on Mo'orea and determined if any of them were parasitoids of *T. tahitiensis*, and this could be a potential direction for future research.

Costs and Benefits of Web-Building

Predation often consists of a series of behavioral decisions leading up to prey capture, and this also applies to web-building spiders (Higgins and Buskirk 1992). Aside from the process of subduing captured prey, a spider would have made most of its predatory decisions during web-site selection and the process of web building (Shear 1986). Therefore, it is extremely important for spiders to build efficient webs which balance energetic investment with fitness payoffs. This is especially the case for *T. tahiensis* spiders since they build relatively costly webs.

In this study, I looked at how dominant substrate, spider size, and maternal state could potentially influence web characteristics in *T. tahitiensis*, but this is only a stepping stone to fully understanding the exact costs and benefits involved with the construction of a web. For example, while certain web characteristics such as diameter in conjunction with number of attachment points improve prey capture, not all spiders build webs which are extremely large with many attachment points due to physical, energetic, physiological or environmental constraints. This indicates that there are several other factors that could affect web characteristics. An example would be the current energy state of the spider, as spiders that have consumed prey reduce their investment into webs as compared to hungry spiders (Sherman 1994). An environmental factor involved could be the presence of other spiders, and spiders may vary their webs in response to conspecifics (Gillespie 1987), and other species of spiders (Enders 1974, Brown 1981). This may be relevant as I have observed some *T. tahitiensis* spiders building webs on the same plant, and also in close proximity to *Leucauge granulata* spiders, which also spin horizontal orb webs. In addition, the type and size of prey captured are different in energy content (Riechert 1991) and could therefore contribute different energetic payoffs, and this was not accounted for in this study. Lastly, other web characteristics not measured such as spacing between web radii (Eberhard 1986) and thread density (Rypstra 1982), could also influence prey capture. Future research looking at all these interactions could further our understanding of the complex relationships involved in the energetic investment and payoffs of *T. tahitiensis* spiders and their webs.

CONCLUSION

Spiders are important predators in tropical ecosystems, and how much they can affect the food web in terms of prey capture depends on their web characteristics. Therefore, understanding how they vary their webs in response to different environmental and physiological factors can also help us understand their impact on insect populations in the forest. My results suggest that prey capture is a function of certain types and combinations of web characteristics, and that foraging and reproductive needs of *T. tahitiensis* spiders are more significant than substrate in influencing web characteristics. This indicates that there is some pattern to the seemingly chaotic variation in web characteristics. This information, combined with information about the diversity of prey *T. tahitiensis* consumes, could be useful in modeling more comprehensive food web interactions.

ACKNOWLEDGMENTS

I thank the class professors - George Roderick, Vince Resh, Patrick Kirch, and Jere Lipps for their advice and guidance, and Rosemary Gillespie for introducing me to *T. tahitiensis* spiders. I am indebted to the graduate student instructors - Virginia Emery, Bier Kraichak, and Jenny Hofmeister for spending too much of their time running the class smoothly and giving detailed feedback on paper drafts. I sincerely thank Faith Chan, Michael Lough-Stevens, and Eric Olliff for reviewing the draft of this paper. I am also grateful to the National Parks Board Singapore for funding some of my class expenses. Lastly, special thanks go to my family and fellow classmates for their help and support.

LITERATURE CITED

Berland L., J. Pellegrin. 1934. Sur une Araignee pecheuse de poissons. Bulletin de la Societe Zoologique de France T **59**:210-212.

Blackledge T. A., R. G. Gillespie. 2004. Convergent evolution of behavior in an adaptive radiation of Hawaiian web-building spiders. Proceedings of the National Academy of Sciences of the United States of America **101**:16228-16233.

Blackledge T. A., J. W. Wenzel. 2001. Silk mediated defense by an orb web spider against predatory mud-dauber wasps. Behaviour **138**:155-171.

Brown K. M. 1981. Foraging Ecology and Niche Partitioning in Orb-Weaving Spiders. Oecologia **50**:380-385.

Chacon P., W. G. Eberhard. 1980. Factors affecting numbers and kinds of prey caught in artificial spider webs, with considerations of how orb webs trap prey. Bulletin of the British Arachnological Society **5**:29-38.

Eberhard W. G. 1971a. Ecology of Web of Uloborus-Diversus (Araneae-Uloboridae). Oecologia **6**:328-342.

Eberhard W. G. 1971b. Senile Web Patterns in Uloborus-Diversus Araneae Uloboridae. Developmental psychobiology **4**:249-254.

Eberhard W. G. 1986. Effects of Orb-Web Geometry on Prey Interception and Retention. Pages 70-100 *in* W. A. Shear, editor. Spiders: webs, behavior, and evolution. Stanford University Press, Stanford, California, USA.

Eberhard W. G. 1990. Function and Phylogeny of Spider Webs. Annual Review of Ecology and Systematics **21**:341-372.

Enders F. 1974. Vertical Stratification in Orb Web Spiders Araneidae Araneae and a Consideration of Other Methods of Coexistence. Ecology (Washington D C) **55**:317-328.

Gillespie R. G. 1987. The Role of Prey Availability in Aggregative Behavior of the Orb Weaving Spider Tetragnatha-Elongata. Animal Behaviour **35**:675-681.

Gillespie R. G., E. M. Claridge, and G. K. Roderick. 2008. Biodiversity dynamics in isolated island communities: interaction between natural and human-mediated processes. Molecular ecology **17**:45-57.

Heiling A., M. Herberstein. 2000. Interpretations of ore-web variability: A review of past and current ideas RID D-2042-2011. Ekologia-Bratislava **19**:97-106.

Heiling A. M., M. E. Herberstein. 1999. The role of experience in web-building spiders (Araneidae). Animal Cognition **2**:171-177.

Higgins L. E., R. E. Buskirk. 1992. A Trap-Building Predator Exhibits Different Tactics for Different Aspects of Foraging Behavior. Animal Behaviour **44**:485-499.

JMP, Version 9.0.0. SAS Institute Inc., Cary, NC, 1989-2011.

Kingsland S. E. 1995. Science and its Conceptual Foundations: Modeling nature: Episodes in the history and population ecology, Second edition. University of Chicago Press, 5801 Ellis Ave., Chicago, Illinois 60637, USA; University of Chicago Press, London, England, 5801 Ellis Ave., Chicago, Illinois 60637, USA; London, England.

Li D. Q., W. S. Lee. 2004. Predator-induced plasticity in web-building behaviour. Animal Behaviour **67**:309-318.

Lomnicki A. 1988. Population ecology of individuals. Monographs in population biology **25**:1-223.

Lubin Y. D. 1986. Web Building and Prey Capture in the Uloboridae. Pages 132-171 *in* W. A. Shear, editor. Spiders: webs, behavior, and evolution. Stanford University Press, Stanford, California, USA.

Martin P.., H. Kraemer. 1987. Individual-Differences in Behavior and their Statistical Consequences. Animal Behaviour **35**:1366-1375.

McReynolds C. N. 2000. The impact of habitat features on web features and prey capture of Argiope aurantia (Araneae, Araneidae). Journal of Arachnology **28**:169-179.

Mcreynolds C. N., G. A. Polis. 1987. Ecomorphological Factors Influencing Prey use by 2 Sympatric Species of Orb-Web Spiders, Argiope-Aurantia and Argiope-Trifasciata (Araneidae). Journal of Arachnology **15**:371-383.

Nentwig W. 1982. Why do Only Certain Insects Escape from a Spiders Web. Oecologia **53**:412-417.
Opell B. D. 1984. Eggsac Differences in the Spider Family Uloboridae (Arachnida, Araneae). Transactions of the American Microscopical Society **103**:122-129.
Opell B. D. 1979. Revision of the Genera and Tropical American Species of the Spider Family Uloboridae. Bulletin of the Museum of Comparative Zoology **148**:443-549.
Riechert S. 1991. Prey Abundance Vs Diet Breadth in a Spider Test System. Evolutionary Ecology **5**:327-338.
Rypstra A. 1982. Building a Better Insect Trap - an Experimental Investigation of Prey Capture in a Variety of Spider Webs. Oecologia **52**:31-36.
Seligy V. L. 1971. Postembryonic Development of Spider Enoplognatha-Ovata (Clerck) (Araneae-Theridiidae). Zoological Journal of the Linnean Society **50**:21-31.
Shear W. A. 1986. Spiders--webs, behavior, and evolution. Stanford University Press, Stanford, California.
Sherman P. M. 1994. The Orb-Web - an Energetic and Behavioral Estimator of a Spiders Dynamic Foraging and Reproductive Strategies. Animal Behaviour **48**:19-34.
Uetz G. W., A. D. Johnson, and D. W. Schemske. 1978. Web placement, web structure, and prey capture in orb-weaving spiders. Bulletin of the British Arachnological Society **4**:141-148.
Venner S., J. Casas. 2005. Spider webs designed for rare but life-saving catches. Proceedings of the Royal Society B-Biological Sciences **272**:1587-1592.
Watanabe T. 2001. Effects of web design on the prey capture efficiency of the uloborid spider Octonoba sybotides under abundant and limited prey conditions. Zoological Science **18**:585-590.

APPENDIX A

Sample Sizes for Web Characteristics and Prey Capture

Web Characteristics	Sample Size
Height	900
Diameter	754
Attachment Points	786
Exposed	898
Slanted	864

Note: Missing samples due to inability to measure web characteristics due to unforeseen circumstances such as wind damage while measuring.

Sample Sizes for Dominant Substrate and Web Characteristics

Dominant Substrate	Sample Size
A. evecta	62
Dead branches	50
I. fagifer seedlings	70
S. malaccense	37
T. wilkesianum	43

Note: Only large, non-maternal spiders were used.

Sample Sizes for Spider Size and Web Characteristics

Spider Size	Sample Size
Large	70
Medium	62
Small	45

Note: Only non-maternal spiders on *I. fagifer* seedlings were used.

Sample Sizes for Spider Maternal State and Web Characteristics

Spider Maternal State	Sample Size
Mother	19
Non-mother	70

Note: Only large spiders on *I. fagifer* seedlings were used.