

2012

Factors Influencing Web Tenure in a Tropical Spider and Comparison between Forest and Non-forest Habitats

Daniella R. Barraza
Scripps College

Recommended Citation

Barraza, Daniella R., "Factors Influencing Web Tenure in a Tropical Spider and Comparison between Forest and Non-forest Habitats" (2012). *Scripps Senior Theses*. Paper 166.
http://scholarship.claremont.edu/scripps_theses/166

This Open Access Senior Thesis is brought to you for free and open access by the Scripps Student Scholarship at Scholarship @ Claremont. It has been accepted for inclusion in Scripps Senior Theses by an authorized administrator of Scholarship @ Claremont. For more information, please contact scholarship@cuc.claremont.edu.

Factors Influencing Web Tenure in a Tropical Spider and Comparison between Forest and Non-forest
Habitats

A Thesis Presented

by

Daniella R. Barraza

To the W.M. Keck Science Department

Of the Claremont Colleges

In partial fulfillment of

The degree of Bachelor of Arts

Senior Thesis in Environmental Science

December 10, 2012

Table of Contents

Abstract	2
Introduction.....	3
Materials and Methods	12
Study Site.....	12
Study Species.....	12
Field Census.....	13
Data Analysis	16
Results	18
Variable Comparisons Between Habitats.....	18
Determinants of Web Tenure.....	24
Relationship among Variables.....	25
Discussion	29
Variable Comparisons Between Habitats.....	29
Web tenure.....	30
Relationship among Variables.....	32
Conclusion	33
Acknowledgments	35
References.....	35

Abstract

Webs are fundamental to the ecology of *Nephila clavipes*, the golden orb-weaver spider, because they serve as sites for prey capture, reproduction, competition, predation, and parasitism. In addition to the presence of the female *N. clavipes*, males and kleptoparasites reside on the web in varying numbers. Webs are also found in clusters with conspecific females. Web site selection and length of web tenure is a behavioral decision vital to the spider's fitness and the ecology of her species. I conducted a field census to quantify these factors and analyze their influence on web tenure, compare web ecology between a forest and non-forest habitat, as well as explain the significance of *N. clavipes*' web as central to many interactions. Web tenure, as well, was influenced differently by the factors between both environments. In the forest habitat, increase in prey capture rate decreased web tenure and inclusion in cluster increased web tenure. In the non-forest habitat, only increase in spider size was related to increased web tenure. There were significant differences between the two habitats in the sizes of the female spider and quantity of males and kleptoparasites. Results also showed that spider size influenced quantity of males and web diameter influenced quantity of kleptoparasites. Explanation of these results can be attributed to the complex relationships among the variables and the consequences of living in habitats impacted by human occupation.

Introduction

To behave appropriately in different contexts and situations, an animal often demonstrates behavioral plasticity rather than a programmed response. It will change its behavior rather than act the same way in any situation. Within its range of evolutionarily-derived behaviors, it is important for the animal to act optimally in relation to different circumstances (Sih et al. 2004). For example, sit-and-wait predators are known to make behavioral decisions regarding their trap design according to environmental cues (Klokocovnik et al. 2012). Spiders are capable of deviating from a programmed response, and alter their behavior to fit the current situation. This can be witnessed in experiments where some spiders were removed from their web during the web construction phase and placed in another unfinished web, but they were still able to complete the web taking into consideration its unfinished state instead of continuing on as if it was the same (Peters 1970). This behavioral plasticity allows them to adjust their behavior or learn from experience (Bays 1962; Leguelte 1969). For example, spiders may alter their web based on foraging experiences, either successful or unsuccessful (Nakata 2007).

For web-weaving spiders, choices about where to establish a web and how long to stay in that location are among the most important flexible decisions they make. Animals choose optimal habitats in relation to their reproduction and survival though sometimes the quality of a habitat depends on the number of competing conspecifics present. (Rosenzweig 1991). With *Nephila clavipes*, the golden orb-weaver spider, this is apparent in the intense competition over building a web next to artificial light where prey are abundant; large *N. clavipes* inhabit this space, and the smaller ones are forced away to less optimal habitats (Heiling and Herberstein 1999). It is difficult to assess what parameters *N. clavipes* looks for while selecting a new web site. A few can be height, vegetation structure, or direction of light (Enders 1977). It is known that spiders can determine at least two abiotic factors: temperature and humidity (Foelix 2011). However, there are a number of

possible factors that influence web tenure and spiders are sensitive to many stimuli. Web spiders are mainly receptive to mechanical stimuli (e.g. vibrations) and chemical stimuli (Foelix 2011). Therefore, studies attempting to tackle the question of how *N. clavipes* chooses a web site are rare because of scarce information. On the other hand, there are numerous studies focused on the question of why *N. clavipes* and other spiders choose to abandon a web. Web abandonment is often translatable to web site tenure because the study of both is the same. Web tenure or web site tenacity is the duration of time spent in a given web, which seems to be influenced by multiple factors. The main ones are prey load (e.g. Vollrath and Houston 1986) and kleptoparasite load (e.g. Higgins and Buskirk 1998; Rypstra 1981). The less studied factors are male load (Rittschof and Ruggles 2010) and the significance of living in a colony or aggregation (e.g. Hodge and Uetz 1996; Blamires et al. 2010). The studies of the latter factor, however, concentrate on how colonies or aggregations affect other factors such as prey load rather than focusing specifically on web tenure. *N. clavipes*' web tenure, web selection and then web abandonment, bring up interesting questions about their habitat selectivity and the complexity of behavioral decisions. In this study, I address the issue of web tenure by quantifying the relationship between web tenure of females and their webs' prey load, male load, kleptoparasite load as well as the clustering of other females near their web.

The web of *N. clavipes* is the site for the confluence of all four factors, and serves multiple purposes. The cost of constructing this device is resource-intensive (Townley and Tillinghast 1988) therefore *N. clavipes* will recycle it by eating it before reconstructing the web or abandoning it (Higgins and Buskirk 1998). *N. clavipes*' web is three-dimensional because it has a barrier in addition to the orb. This type is referred to as the orb and barrier web or just barrier web (Grostal and Walter 1999). The barrier web and other similar webs are habitats for these species and are constructed as prey-catching devices. They serve as a site for reproduction, parasitism, competition, and predation. Therefore, the ecological importance of the web results in an important decision that must be made

by *N. clavipes*, that is, how long to remain on a given web, which will affect her fitness and, ultimately, the fitness of other individuals, like males and kleptoparasites that also use the females' webs.

First of all, prey is the most studied factor concerning its influence on web tenure because of its apparently obvious weight in *N. clavipes*' web tenure decision, but so far no consensus has been reached (e.g. Rypstra 1981; Vollrath 1985). Prey capture rate did not differ between spiders with short or long web tenure (Rypstra 1981), and both fed and starved spiders had long web tenures (Vollrath 1985). Common preys caught in the webs are from the order of Diptera and Coleoptera with four saprophagous families (Hénaut et al. 2010). *N. clavipes* do not consume all of the prey trapped by their webs; they normally discriminate by prey size. An initial screening of prey is done by the mesh size of their webs. Larger mesh sizes capture large prey while letting smaller prey pass through. This mesh size is positively correlated with size of spider (Moore 1977). Despite lack of consensus over degree of importance of prey in web tenure, the predator-prey interaction does influence *N. clavipes*. Spiders will produce webs varying in thread length, web stickiness, and surface area contingent on prey detection or prey capture information (Nakata 2007). Similarly, increase in prey density was linked with increase in spider density (Rypstra 1983).

The starkly dimorphic, much smaller, males do not spin their own web, although they are capable of doing so (Moore 1977) which is why they reside on the female's web. They travel the area until they find the chemical scent of a nearby female (Willey and Jackson 1993), and usually approach female spiders nearing adulthood (Christenson et al. 1985). Male presence is desired by females for reproduction and multiple males provide multiple mating opportunities (Rittschof and Ruggles 2010); but there are also energetic costs. Multiple males can be found residing on the web of the female with the dominant male nearest the hub of the orb (Vollrath 1980). This results in competition over copulation with the female and in attempts by the winner to mate with her while

she is eating or when she is not disposed to mating. This harassment presumably affects her nutritional intake, but also directly, males will attempt to feed on caught prey items (Christenson et. al 1985). In at least one study, male presence was linked to large kleptoparasites loads. A probable reason is that female distraction by the male is advantageous to the parasites (Grostal and Walter 1999). In addition, males feed on the female's prey which negates her exertion in subduing the prey and eliminates a source of nutrition. Energy is very important for spiders because they have very little to spare; spiders must recover for hours after minutes of high activity (Foelix 2011). In the case of *Geolycosa missouriensis*, after 30 seconds of exercise its heart rate increased from 48 beats per minute to 176 (Sherman and Pax 1968). Therefore, the costs and benefits of male presence or the effect of passing an unknown threshold on male density might influence her decision to abandon her web site.

While the presence of males may benefit females, organisms that truly negatively affect *N. clavipes*' fitness are kleptoparasites. Kleptoparasites are usually from the genus *Argyrodes*. They are small silvery or brown spiders that reside in the barrier of the web and only venture onto the orb to feed on prey items. Thus, because it impacts nutritional intake, kleptoparasite load should factor into *N. clavipes*' web abandonment decision. A positive correlation between kleptoparasite load and web abandonment highlights this relationship. Webs with a high kleptoparasite load significantly affected nutritional intake of the female which then compels her to search for a site with more optimal conditions (Rypstra 1981). Furthermore, kleptoparasites steal not only prey, but also silk. Kleptoparasites were observed cutting up to 4 cm of silk from the web for ingestion (Higgins and Buskirk 1998). The females loses the previously invested resources from the silk since, as mentioned before, she recycles her web. The holes that appear due to this parasitism also change the design of her web. They reduce the surface area used to trap prey and destabilize the web (Grostal and Walter 1997). The female must then repair the damage or leave it in a degraded condition. Aside

from these consequences, kleptoparasites can directly affect the fitness of the female by preying upon her (Larcher and Wise 1985). The kleptoparasitic cost is therefore likely to influence web tenure.

Other participants in the ecological web of *N. clavipes* are neighboring females—conspecific and/or interspecific species. A previous study of *N. clavipes* did not include colonial living or aggregation in their research in relation to other factors and their collective effect on web tenure (Rittschof and Ruggles 2010). However, multiple studies do exist surrounding this surprisingly social aspect of *N. clavipes*' otherwise solitary life. I define an aggregation or colony as a group of webs in close proximity or sharing anchor lines with the term “aggregation” referring specifically to a group of intraspecific spiders and “colony” referring to a group of conspecific spiders (Hodge and Uetz 1992). In this study, however, I only took into account colonies not aggregations. Existing in a solitary state, in a colony, or aggregation may take part in *N. clavipes*' decision over web abandonment, but this particular factor is more complicated as it affects the other three factors of male presence, kleptoparasite load, and foraging efficiency. In fact, the focal point of multiple studies is how the singular or associative nature of *N. clavipes* is linked to these three factors rather than to the female spiders themselves (e.g. Rypstra 1981; Vollrath and Houston 1986). Of course, this does not imply that the three factors act exclusively on web tenure. There could be interactions between clustering and each of the factors mentioned above, prey capture rate, male presence and kleptoparasite numbers, such as male presence differing between clustered and singular webs and therefore leading to differences in web tenure. My study investigates if the effect of these factors is significant to *N. clavipes*' decision process and if there is a hierarchy of priorities. Again, it is hard to pry apart the ecosystem of *N. clavipes*' because all of the quantifiable aspects may interact with each other.

To begin with, Mexican populations of *N. clavipes* experience lower predation when in aggregations of *Metepeira incrassata* than when solitary (Hodge and Uetz 1992). Potential explanations included hesitation from predators to weave through webs and depredate clusters of spiders, and the early-warning system. When danger approaches, vibrations are transmitted throughout the connecting webs alerting the hosts to retreat to safety. Large spiders are especially insulated from danger because they reside in the middle of the colony, benefiting from what is called the “selfish herd” effect (Rayor and Uetz 1990). Moreover, the probability of a predator encountering a solitary spider or a cluster is equal, but being part of a cluster lessens the chances of being chosen for prey. This effect is called risk dilution (Uetz and Hieber 1994). At the same time, living in a group can entail some costs, such as enhanced visibility to predators (Vulinec 1990). From this perspective, it can be said that spiders will move towards clusters or that they will move away from clusters when a threshold of cluster size is reached that makes the benefits of clustering less than the costs.

While less predation is a potential benefit of forming clusters, the increase of kleptoparasite abundance is energetically costly. Webs are analogous to habitat patches where clusters are interconnected islands (Agnarsson 2003). The interconnectivity of these islands or webs allows the migration of kleptoparasites from web to web which increases the overall kleptoparasite load relative to the load encountered in solitary webs. For kleptoparasites inhabiting clusters of webs, the risk of being deprived of prey supply and home due to the death of a solitary spider or her movement is minimized. Clusters offer more stability because the other webs will provide a substitute residence, and clusters appear to be long-lasting (Agnarsson 2003). As a result, a new web in a cluster will be rapidly colonized since the neighboring webs function as sources of kleptoparasites (Miyashita 2001). Competition between kleptoparasites over limited space is not

only alleviated by new webs, but by spider molting. As spiders grow so do their webs (Agnarsson 2003), which increase in size and allow for kleptoparasite arrivals or redistribution.

Clustering can also interact with prey load to influence web tenure (Blamires et al. 2010; Mestre and Lubin 2011). In more social spiders, colonies increase both prey load and prey size (Yip et al. 2008). Because colonies are a large tangle of silk, prey have less chances of escape or a “ricochet effect” occurs (Uetz 1989). The opposite argument can be posited in that prey load is the cause of colonies rather than the effect (Uetz 1988). Spiders tend to form colonies in times of high prey abundance, and to separate when abundance is low. This is supported by the fact that cluster-forming spiders reside in tropical regions which support high insect biodiversity and abundance (Mcrate and Uetz 2010) However, there are at least two studies that conflict with these results, finding that prey load has no effect on web tenure (Vollrath and Houston 1986; Leborgne et al. 1998).

One more layer to uncover is how these factors change from a natural environment to an environment with human characteristics (i.e. spiders that build webs around buildings and outside of the forest). Delving into the literature reveals little on the intersection of anthropogenic habitats and spiders’ fitness. There are studies about spider diversity on the urban-to-rural gradient (e.g. Pinkus-Rendón et al. 2008; Shochat et al. 2004 and the response of spiders to forest fragmentation (Miyashita et al.1998; Kapoor 2008). One of these studies found that prey load changes in forest fragments, citing the decrease in large prey abundance as the cause of decreased insect diversity (Miyashita et al. 1998). A final part of my study is to investigate how the four factors described above differ in webs constructed around man-made structures compared to those in nearby forest within a tropical environment.

This study was undertaken to assess the importance of prey load, male load, and kleptoparasite load to *N. clavipes*’ decision on web tenure in addition to the influence of clustering.

The roles these factors have in the ecology of *N. clavipes* are intricate and well-recorded by some previously published papers, but no study has simultaneously in one population examined their influence on web tenure. I hypothesized that the increase of kleptoparasite load and male load would reduce web tenure because of their overall negative impact on *N. clavipes*' fitness.

Alternatively, I hypothesized that inclusion in a cluster and increased prey load would elongate web tenure because of additional safety benefits and of the overall positive impact on prey capture as a result of greater surface area in clusters and the essential nature of prey on survival. Additionally, one question that has not been adequately addressed in the literature is the influence of anthropogenic habitat on the success and behavior of *N. clavipes*. Included in my study is the distinction between spiders residing in the forest or around buildings lacking significant vegetation.

Finally, I hypothesized that compared to forested webs, in non-forest habitats, prey load would increase and male load and kleptoparasite load would decrease and colonies would be more common. Artificial lights attract more prey items and, because of space constraints, spiders should be forced into more colonies. Kleptoparasite load and male load will decrease because they will not venture out of the forest and will be unable to detect any chemical signals from the female.

Therefore, I hypothesized that spider size would be bigger in the non-forest habitat because of the better conditions, and that spider size and web diameter would be closely correlated. To further underline the importance of the web in the ecology of *N. clavipes*', I study how prey, males, and kleptoparasites interact with the web and the spider, distinguishing between both habitats. I

hypothesized that prey and kleptoparasites would be present in greater numbers in larger web diameters because of greater space availability; males would be present in greater numbers depending on spider size, an indicator of age, because they copulate with adults females; and cluster would not be related to either spider size nor web diameter. Lastly, in the non-forest environment, prey, males, and kleptoparasites would only be affected indirectly by differences in

spider size and web diameter between both habitats as I formerly mentioned. In other words, I analyze (1) differences between number of prey, males, kleptoparasites, clusters, spider size, and web diameter between both habitats; (2) effect of prey, males, kleptoparasites, and cluster on web tenure differentiating between habitat type, and (3) how number of prey, males, kleptoparasites, and cluster are influenced by spider size or web diameter. To test these hypotheses I conducted a census of the *N. clavipes* population in the tropical forest of Costa Rica at the Firestone Center for Restoration Ecology. With my findings I hope to help complete our understanding of the complexity of these behavioral decisions, particularly in spiders, and to gather more information about urban ecology research for arachnids.

Materials and Methods

Study Site

Censusing of *Nephila clavipes* occurred from June-July of 2012 between the hours of 0600 and 1200 on Pitzer College's Firestone Center for Restoration Ecology (FCRE), a reserve and field station. It adjoins the Hacienda Barú Reservation and is located approximately 150 km south of San José, Costa Rica (83°51'40"S, 9°16'44"E). The reserve is 150 acres of tropical rainforest, mainly secondary forest, with mixed vegetation due to its past history as a farm for cattle and then for crops. It comprises several habitats: bamboo forest, banana plantation, riparian forest along the creeks, and secondary forest growth. There are trails crossing the reserve and along the perimeter. This makes it easier to locate the female spiders because they prefer open spaces along the edges of the forest and it allows for easier access. The *N. clavipes*' webs were found in both native and non-native vegetation as well as adjacent to buildings associated with the FCRE, which were the non-forested webs.

Study Species

During the summer, *Nephila clavipes* undergo rapid growth. Spiderlings emerge from their egg case in early summer. They form a tangle web near their web case before dispersing. They continue to molt until they reach maturity and the females lay their eggs in the fall (Moore 1977). Consequently, most of the spiders in my sample were immature females, and I could not definitively label a female as an adult. Though *N. clavipes*' web is classified as an orb and barrier web, the orb is not a complete circle. Instead, it is bottom-heavy with the top of the circle missing. The hub, where the female spends the majority of her time, is closest to the top instead of being perfectly centered, as it normally is in most orb and barrier webs. The barrier is a tangle of silk on one side of the orb. The female spider sits on the hub with the barrier on her dorsal side. While the female is on the hub,

she is alert for vibrations to detect prey edibility or danger and initiate an appropriate behavioral response (Robinson and Mirick 1971).

Field Census

Webs were classified into three areas depending on the purpose of the analysis. For web tenure analysis, I searched along the forest trails in an established transect. For comparison of web tenure between forest and non-forest, I searched in a 3 X 3 meter plot measured in the forest and I searched for webs around the structures in the reserve. Censuses for comparing the forest plot and webs around man-made structures were done June 21 through the end of the census.

I searched for new webs every day and then revisited them every other day. When encountering a new spider and her web, I assigned them an identification number, marked the location with flagging tape, and mapped it using the GIS CyberTracker software on the Juno® Handheld Device from Trimble (Table 1; Fig. 1). I then measured them along the vertical diameter of the orb. The female spider's cephalothorax was measured at the widest point using digital calipers (General®). For spiders found in the forest plot and around man-made structures, they were uniquely marked on the abdomen with enamel paint for easier identification (Testors®). Initial data collection included recording the number of males, kleptoparasites, and prey present in the web, which was also assessed each time I visited a web. I also recorded the number of legs the female *N. clavipes* had (as an indicator of the spider's health) and the number of conspecific females present if the web was clustered (Table 1). A cluster was classified as such if the webs shared an anchor line, had been sharing an anchor line, or was in close proximity to each other (within approximately 1 meter apart).

Initially, all the spiders were uniquely marked to relocate them after they had moved. However, it was not realistic to find spiders in the forest after they had moved because it is not

known how far they travel. Therefore, spider marking was scaled back to include only the forest plot and webs around man-made structures. Only a few of the marked spiders were found after they abandoned their initial web and moved to a new location. Most of the time, solitary and clustered spiders rearranged their webs by a few centimeters. This was not considered a significant move. If a spider moved and I located its new web, the web diameter was re-measured, but the spider was not. Also, webs were only measured once upon initial finding. This can possibly be problematic because spiders molt around 6 times (Moore 1977), and therefore, expand their web size.

Included in the kleptoparasite count were heterospecific females who shared anchor lines with the female *N.clavipes*. Prey count included prey stored on the orb, prey caught during observation, and prey carcasses stored in the barrier. Web tenure was measured from the day the spider was found until the spider disappeared. This is an estimate of web tenure because the exact day the spider arrived at a new web site is not known. Site abandonment is not exact either since webs were checked every other day excluding Sunday. This is still considered an acceptable method for estimating relative web tenure with large sample sizes (Rittschof and Ruggles 2010).

Additionally, condition of the webs were noted and updated constantly, but they were not associated with a given day. This means that there is only one record of web condition per web. A web was considered good if it was a complete web with no major holes; it was fair if it had one hole taking up one quarter of the web; and it was considered poor if the orb was missing. This information and number of legs as an indicator of fitness, in the end, was not included in the analyses.

Table 1. Summary of type of data collected and frequency of collection.

Data type	Collected once	Collected every day
Cephalothorax width (mm)	X	
Web diameter (m)	X	
Location information	X	
Web condition		X
# of male <i>Nephila</i>		X
# of kleptoparasites		X
# of prey		X
# of neighboring female <i>Nephilas</i>		X
# of legs a female <i>Nephila</i> had		X

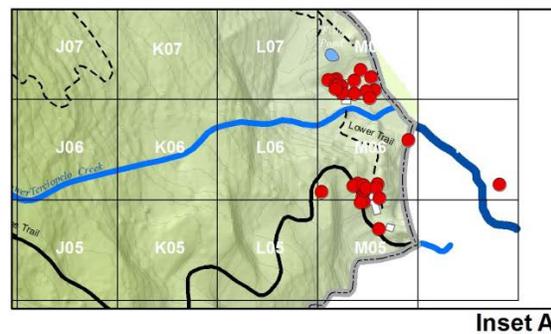
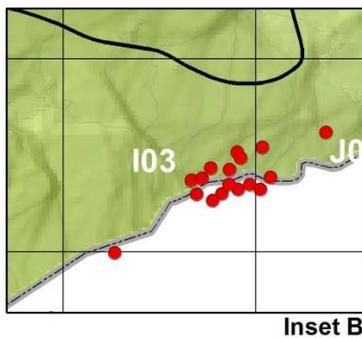
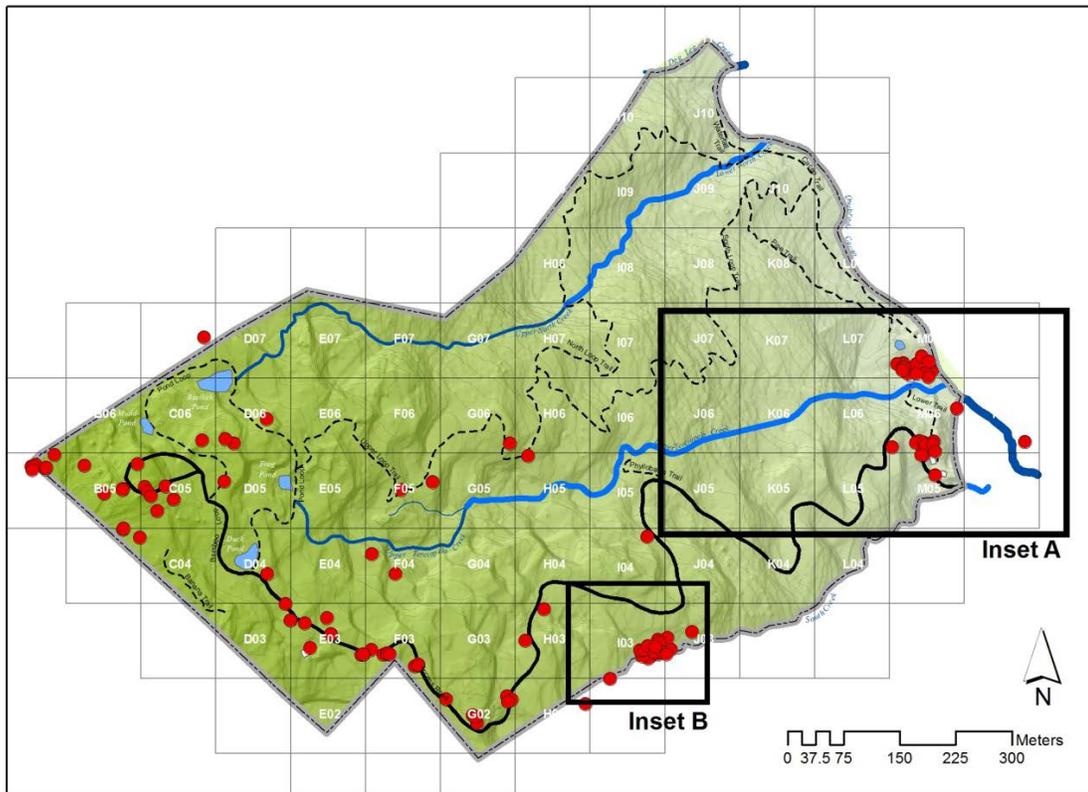


Figure 1. Aerial image of the FCRE showing web site locations. Inset A indicates location of man-made structures, and Inset B indicates location of forest plot.

Data Analysis

For data collected on each web, the numbers were averaged across the number of days observed and described through central tendency measures, either the mean or median, chosen depending on whether a particular variable was normally distributed or not. Prey, male, and kleptoparasite numbers are not continuous, so the mean value was chosen. They are count data and are labeled as categorical. Their distributions were graphed separately according to habitat type. Spider size and web diameter are described through the mean value because they are continuous variables. A correlation test was run on the log transformed data for spider and web diameter separated by habitat type to explain the degree of relation between spider size and web diameter. Cluster type was determined by the number of females in the cluster. I characterized the relative size of each spider in the clusters. Cluster type distribution was graphed separately by habitat type. Each spider within the cluster was ranked by size whether they were the small, medium, large, or largest spider, depending on how many spiders were in the cluster. I used a Mann-Whitney U test to compare the median number of prey, males, and kleptoparasites between the two habitats: forest and non-forest. Comparison between spider size and web diameter in the forest and non-forest habitats was also made by running a two-tailed t-test.

For web tenure analysis, I conducted a generalized linear model (GLM) with Tweedie distribution and loglinear link. This is the best way to model this because the independent variables are mixed, categorical (prey, males, kleptoparasites) and continuous (spider size). The outcomes I was measuring are counts and not enough values were observed to treat them as continuous data. The GLM weighs the effects of independent factors on web tenure by excluding or including different factors until it finds the best fit model. Web tenure, or duration in days, was the dependent variable; whether the spider was in a cluster or not was the categorical fixed factor; median number of prey, males, kleptoparasites, and spider size were the covariates; with

interactions between cluster and prey, cluster and spider size, cluster and kleptoparasites, and cluster and males. Analysis was done separately between forest and non-forest habitats and variables were removed sequentially in a backward stepwise fashion.

Finally, to identify how the number of prey, males, and kleptoparasites are influenced by spider size or web diameter, I ran a GLM with Poisson distribution and loglinear link. A Poisson distribution was chosen because the variables are count data. In this case, the independent variables are not mixed because the model is being run at different times with different variables. The fixed factor was “cluster”, if the spider was solitary or clustered. For prey, I ran the model with web diameter as the covariate, cluster as a fixed factor and the interaction between cluster and web diameter. For male *N. clavipes*, I included spider size as the covariate, cluster as a fixed factor and their interaction, and excluded outliers. For kleptoparasite load, I ran the model with web diameter as the covariate, again with cluster and the interaction between clustering and kleptoparasites. Non-significant interactions and factors were removed from the models.

Table 2. Summary of statistical analyses.

All analysis were split between forest and non-forest		
(1) Variable comparisons Between Habitats	(2) Web tenure analysis	(3) Relationship among Variables
<ul style="list-style-type: none"> • Spider Size & Web Diameter <ul style="list-style-type: none"> ○ Correlation Test ○ 2-tailed t-test* • Cluster <ul style="list-style-type: none"> ○ Graph, no test • Prey, males, kleptoparasites <ul style="list-style-type: none"> ○ Mann-Whitney U test 	Generalized linear model with Tweedie distribution and loglinear link. <ul style="list-style-type: none"> -Fixed factor: clustered or not -Covariates: prey, males, kleptoparasites, spider size -Interactions: cluster & prey, cluster & males, cluster & kleptoparasites, cluster & spider size 	Generalized Linear Model with Poisson distribution and loglinear link. <ul style="list-style-type: none"> -Fixed factor: clustered or not • Prey: Covariate is web diameter; interaction between cluster and web diameter • Male: Covariate is spider size; interaction between cluster and spider size, excluded outliers • Kleptoparasites: Covariate is web diameter; interaction between cluster and kleptoparasite, non-significant interactions were removed

*In SPSS, this analysis was not split, but was a comparison between forest and non-forest habitat.

Results

Variable Comparisons between Habitats

Spider size ranged from 0.62 mm to 7.62 mm in the forest environment and from 0.68 mm to 3.98 mm in the non-forest environment (Fig. 2). Web diameter ranged from 0.06 m to 0.58 m in the forest environment and from 0.10 m to 0.51 m in the non-forest environment (Fig. 3). After log transformation, the data for spider size in forest (Shapiro-Wilk: $w=0.979$, $p=0.368$, $df=63$), spider size in non-forest (Shapiro-Wilk: $w=0.936$, $p=0.179$, $df=21$), web diameter in forest (Shapiro-Wilk: $w=0.972$, $p=0.159$, $df=63$) and web diameter in non-forest (Shapiro-Wilk: $w=0.977$, $p=0.869$, $df=21$) became normally distributed. There was positive correlation between spider size and web diameter in the forest and the non-forest habitats (forest: $r=0.652$, $p<0.0001$, $n=63$; non-forest: $r=0.734$, $p<0.0001$, $n=21$).

The median number of prey per web ranged from zero to two prey per day in the forest and non-forest environment (Fig. 4); the median number of males per web ranged from zero to three per day in the forest environment and from zero to one in the non-forest environment (Fig. 5); and the median number of kleptoparasites per web ranged from zero to ten per day in the forest environment and from zero to four in the non-forest environment (Fig. 6). Between the forest and non-forest environments, there was no significant difference in the median number of prey ($U=731.500$, $p=0.837$, $df=1$; Fig 6). However, significant differences existed in the other two variables. There were significantly more males and kleptoparasites in the forest than in the non-forest webs (males: $U=604.500$, $p<0.043$, $df=1$; Fig. 7; kleptoparasites: $U=432.000$, $p<0.002$, $df=1$; Fig. 8). Since spider size and web diameter are not normally distributed, they were log transformed. After transformation, the Levene's test showed equality of variances in spider size ($F=1.089$, $p=0.300$, $df=85$) and in web diameter ($F=0.020$, $p=0.889$, $df=83$). Between the two habitats, spiders were

significantly smaller in the non-forest habitat than in the forest habitat, but web diameters did not differ significantly ($t=2.364$, $p<0.020$, $df=85$; Fig. 9; $p=0.446$, $t=0.766$, $df=83$; Fig. 10).

N. clavipes females were found in clusters ranging from two to four in the forest environment and were found only in clusters of two spiders in the non-forest environment (Fig. 4). For spiders found in a cluster, there was typically a visible size rank with a small, medium, and large spider (Fig. 5). In the forest environment, 50 spiders were solitary (54.9%), 20 spiders were in clusters of two (22%), nine spiders were in clusters of three (9.9%), and 12 spiders were clusters of four (13.2%). In the non-forest environment, 17 spiders were solitary and 16 spiders were in clusters of two (roughly 50% each).

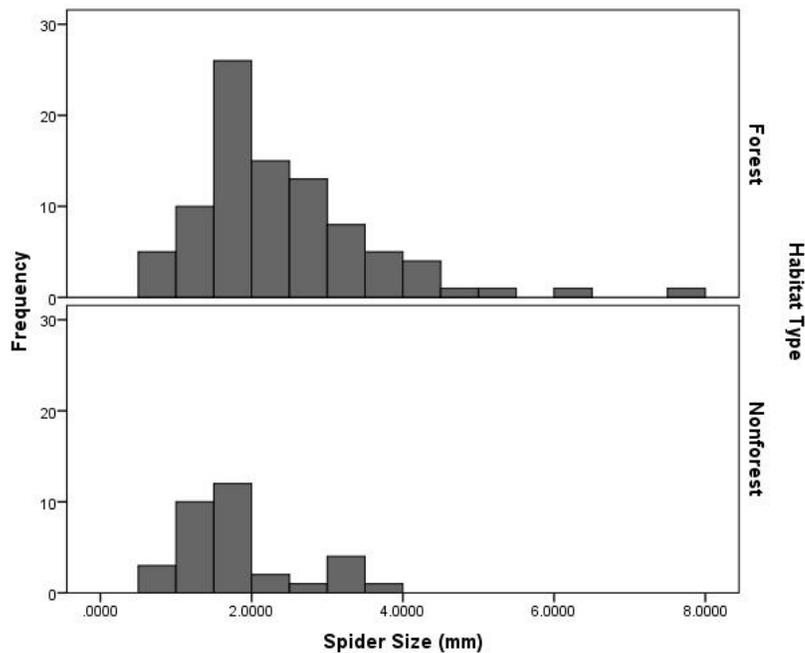


Figure 2. Spider size distribution in forest (n=90) and non-forest habitats (n=33).

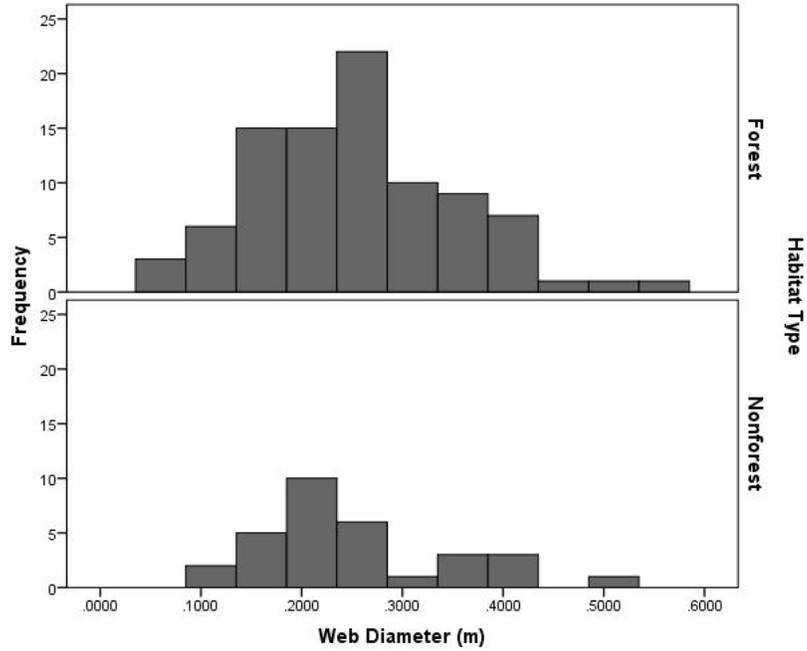


Figure 3. Web diameter distribution in forest (n=90) and non-forest habitats (n=31).

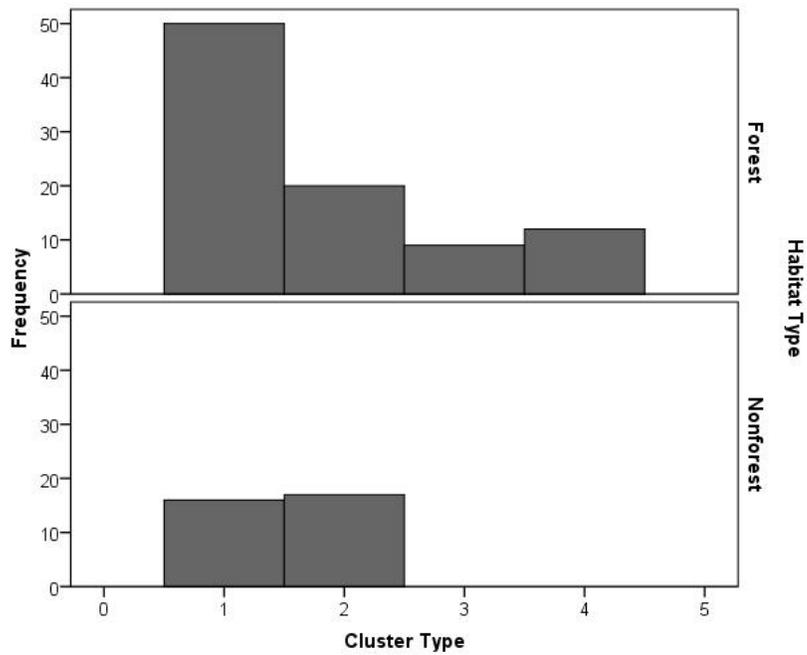


Figure 4. Distribution of cluster types (number of females present in the cluster) in the forest (n=91) and non-forest habitat (n=33).

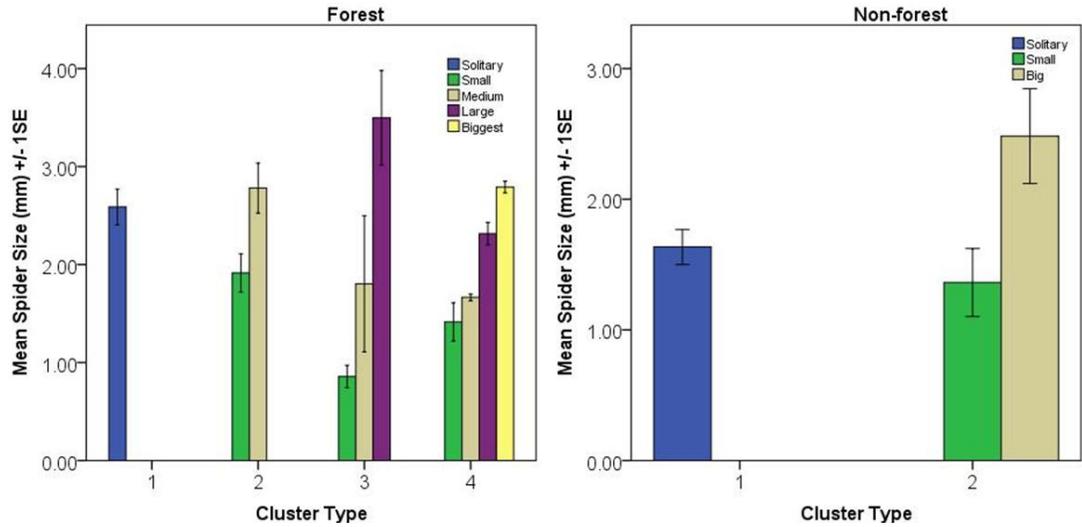


Figure 5. Mean \pm SE spider size within each cluster type indicating its size rank. The cluster of one contains only the mean values for the solitary spider and is not ranked. Forest: solitary cluster (n=50), cluster of two (n=20), cluster of three (n=9), cluster of four (n=12); Non-forest: solitary cluster (n=17), cluster of two (n=16), cluster of three (n=0), cluster of four (n=0).

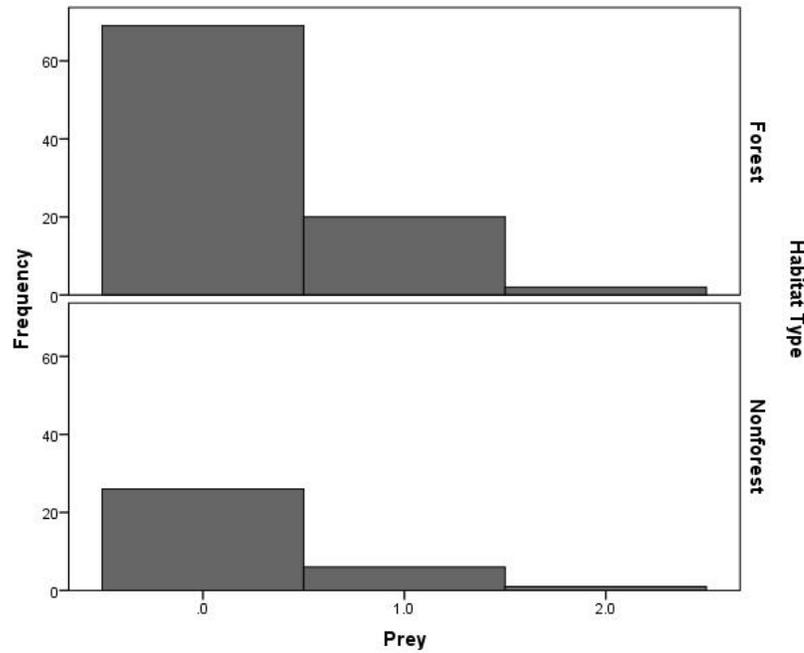


Figure 6. Distribution of median number of prey found per day in webs located in the forest (n=91) and non-forest habitat (n=33).

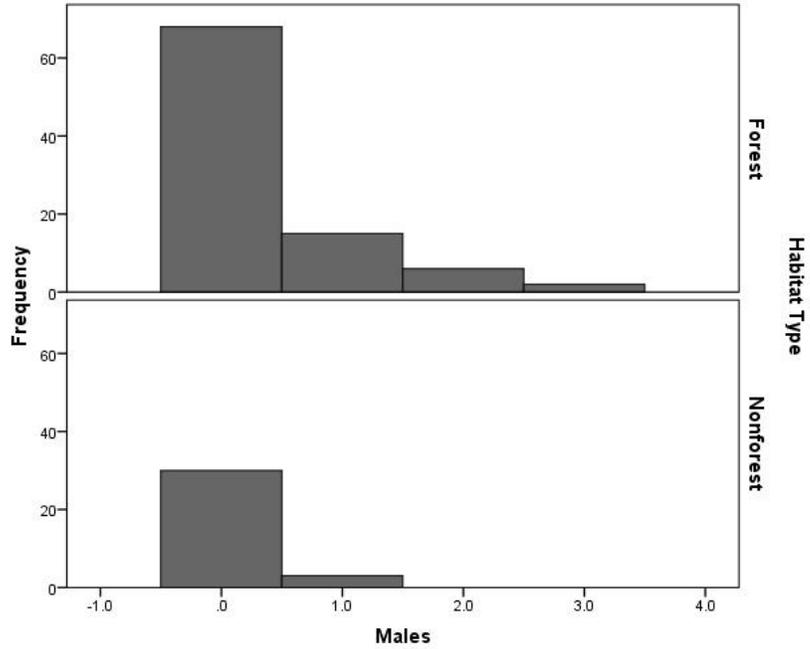


Figure 7. Distribution of median number of males found per day in webs located in the forest (n=91) and non-forest habitat (n=33).

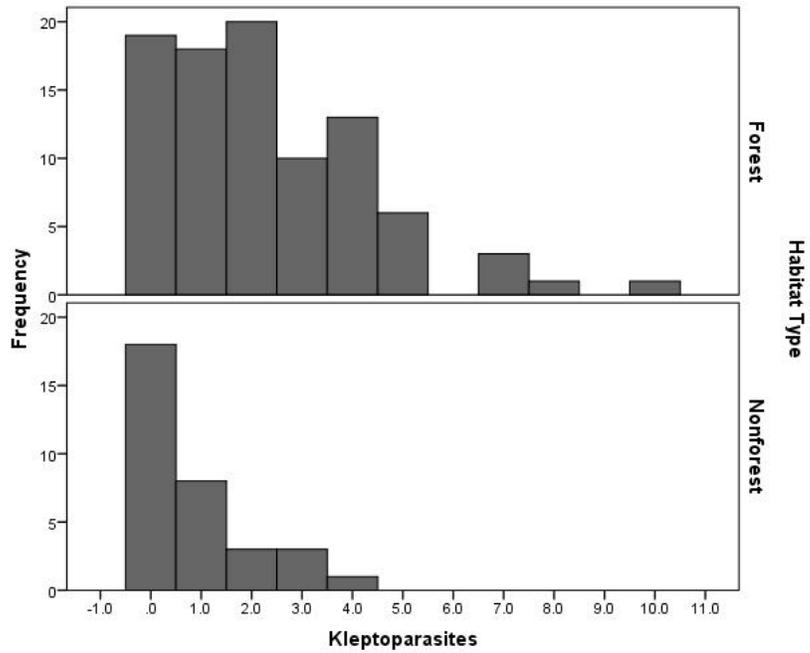


Figure 8. Distribution of median number of kleptoparasites found per day in webs located in the forest (n=91) and non-forest habitat (n=33).

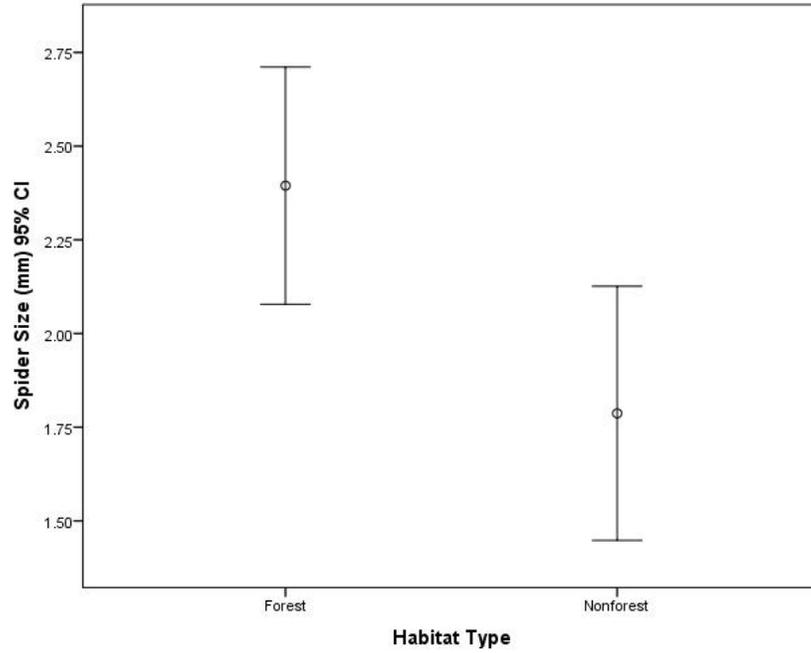


Figure 9. Mean spider size (with 95%CI) in the forest (n=91) and non-forest environments (n=33).

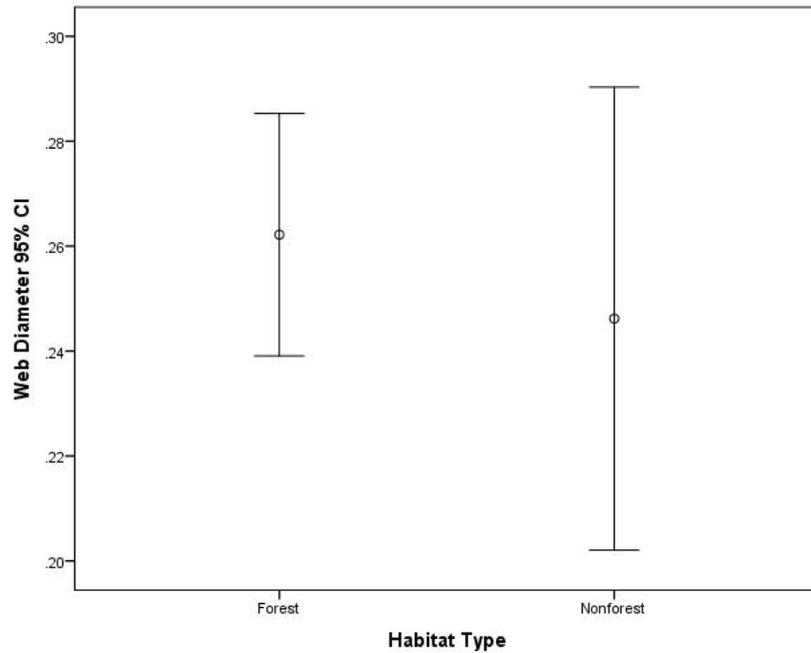


Figure 10. Mean web diameter (with 95%CI) in the forest (n=91) and non-forest environments (n=33).

Determinants of Web Tenure

According to the GLM with Tweedie distribution and loglinear link, web tenure in the forest was significantly affected by number of prey (Wald $\chi^2=4.89$, $p=0.027$, $df=1$; Fig. 11) and whether the spider was in a cluster (Wald $\chi^2=0.709$, $p=0.008$, $df=1$; Fig. 12), but not by the other variables: spider size (Fig. 13), male load, nor kleptoparasite load. Spiders with no prey on most days had greater site tenacity than spiders with one or two prey items (Fig. 11). This effect tended to be significant even when the one spider that caught 2 prey was removed (Wald $\chi^2=3.18$, $p=0.07$, $df=1$). Likewise, spiders found in a cluster had greater site tenacity than solitary spiders (Fig. 12).

In the non-forest habitat, web tenure was significantly related to spider size (Wald $\chi^2=4.985$, $p<.026$, $df=1$; Fig. 13). Larger spiders had greater site tenacity, but prey load nor clustering influenced web tenure (prey: Wald $\chi^2=0.847$, $p=0.358$, $df=1$, cluster: Wald $\chi^2=1.425$, $p=0.233$, $df=1$; Fig. 13).

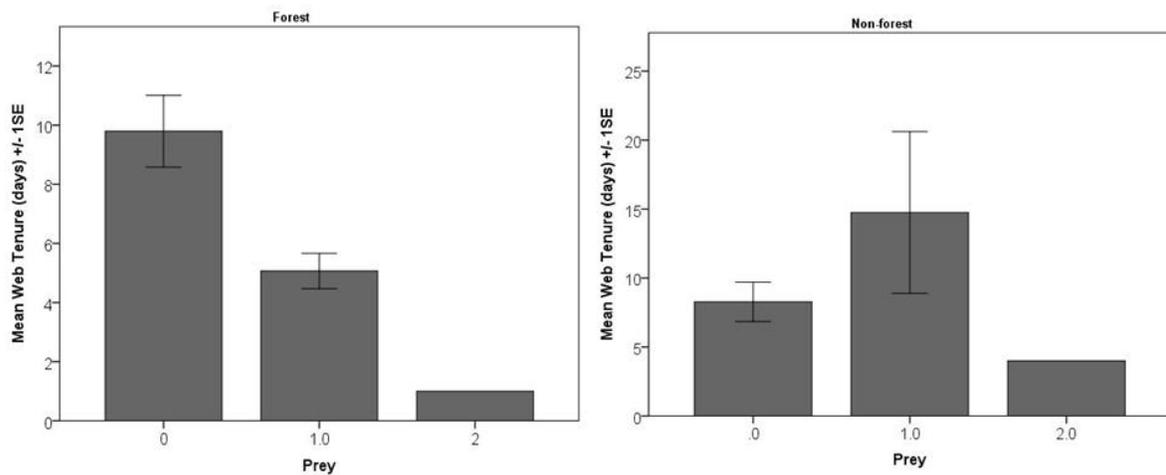


Figure 11. Relationship between web tenure and median number of prey items in the forest captured per day in the forest ($n=65$) and non-forest environment ($n=23$).

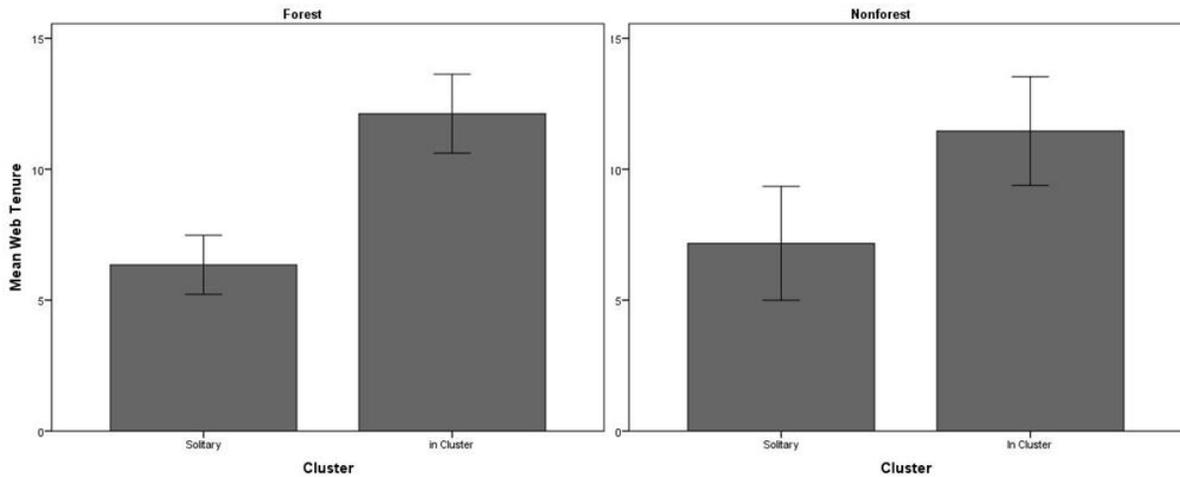


Figure 12. Relationship between mean \pm SE web tenure and clustering in a forest (n=65) and non-forest environment (n=23).

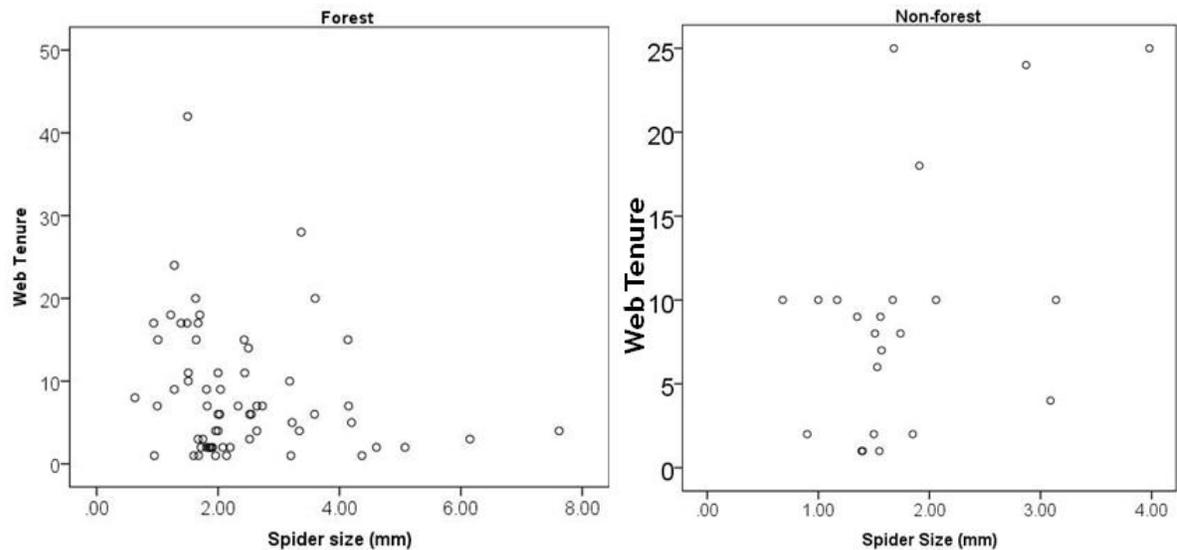


Figure 13. Linear relationship between web tenure and spider size in the forest (n=65) and non-forest environment (n=23).

Relationship among Variables

In a GLM with a Poisson distribution and loglinear link, I found that web diameter had a significant positive relationship with prey load in the forest environment (Wald $\chi^2=5.629$, $p=0.018$, $df=1$), but only tended to in the non-forest environment (Wald $\chi^2=3.813$, $p=0.051$, $df=1$). While the relationship was positive, web diameter explained only around 20% of the variation in prey captured by webs in both habitats (Fig. 14). Prey load did not differ between clustered and non-clustered

webs nor was there a significant interaction between web diameter and cluster in either habitat (cluster forest: Wald $\chi^2=0.260$, $p=0.610$, $df=1$, cluster non-forest: Wald $\chi^2=3.601$, $p=0.058$, $df=1$, interaction, non-forest: Wald $\chi^2=3.502$, $p=0.061$, $df=1$). The interaction between web size and cluster in the forest habitat was not calculated because of numerical difficulties.

There was a significant interaction effect on the median number of males present between spider size and whether a web was clustered in the forest environment (Wald $\chi^2=5.508$, $p=0.019$, $df=1$). For both clustered and non-clustered spiders in the forest environment, there was an increase in males as spider size increased; however, this upward trend was more strongly accounted for in the clustered webs (cluster: $r^2=0.341$; noncluster: $r^2=0.072$; Fig. 15). I did not run the analysis in the non-forest environment because there were not a sufficient number of males recorded.

There was also a significant interaction effect between web diameter and clustering on kleptoparasite load in the forest environment (Wald $\chi^2=3.933$, $p<0.047$, $df=1$). Kleptoparasites were attracted to larger webs, but more so in the clustered webs than in the solitary webs (cluster: $r^2=0.341$, non-cluster: $r^2=0.395$; Fig. 16). In the non-forest environment, the interaction effect was not significant, so it was removed. In this case, neither clustering nor web diameter had a significant effect on the median number of kleptoparasites present on a web (clustering: $\chi^2=1.266$, $p=0.261$, $df=1$; web diameter: $\chi^2=0.682$, $p=0.409$, $df=1$; Fig. 16).

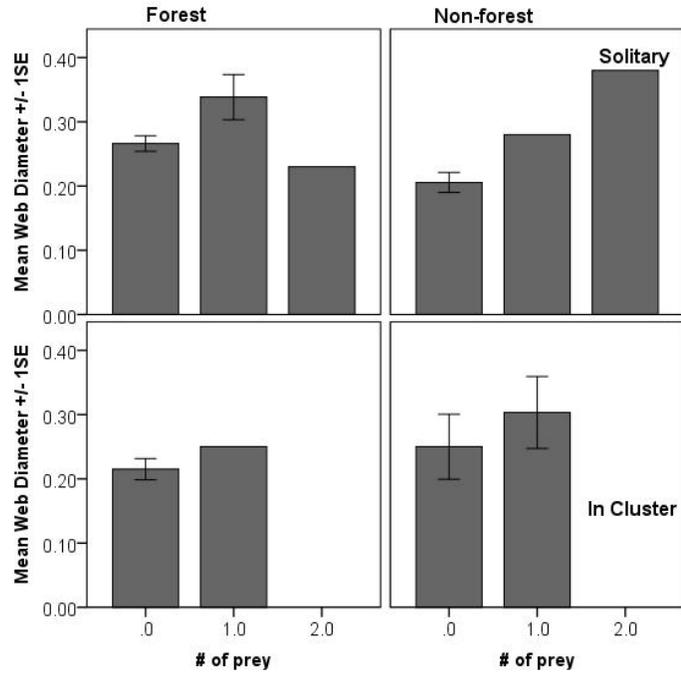


Figure 14. Relationship between web diameter on prey load without effect of clustering in forested (n=64) and non-forested habitat (n=21).

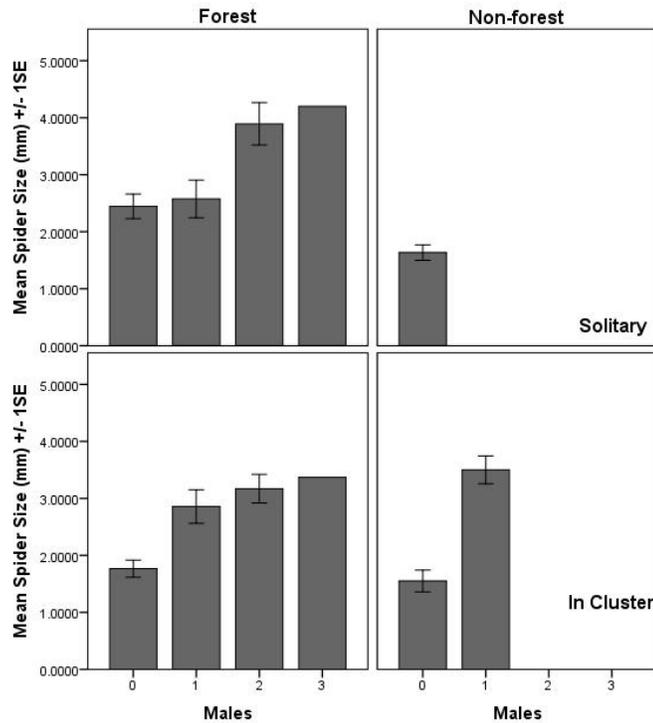


Figure 15. Effect of spider size on male load in the forest environment (n=64). Only one web in the non-forest habitat had a male (n=21).

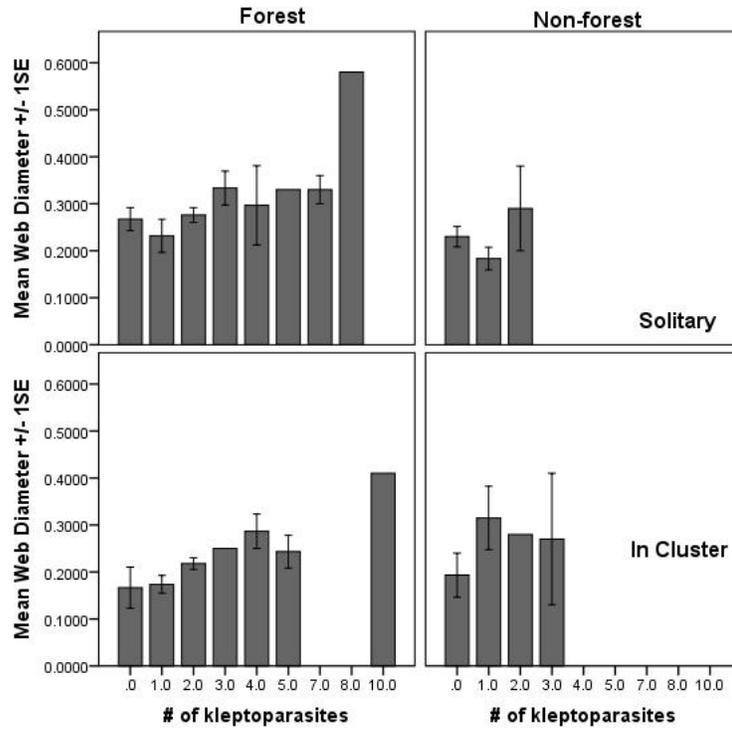


Figure 16. Effect of web diameter on kleptoparasite load in the forest (n=64) and in the non-forest environment (n=21).

Discussion

Variable Comparisons Between Habitats

Calculating the statistical difference between habitat types in the rates of the prey, male, and kleptoparasite, revealed that males and kleptoparasites were less common in webs in the non-forest habitat. This supports my hypothesis that male and kleptoparasite load would decrease in webs in the non-forest habitat. A possibility for these lower numbers of males and kleptoparasites is their hesitation to walk across large open areas in pursuit of the chemical scent of a female *N. clavipes* since they are much smaller than the female spider, perhaps making them more vulnerable to depredation in a more open environment relative to larger females. After all, male *N. clavipes* suffer high mortality rates during travel (Vollrath 1980). At the same time, prey capture rate was not different between the habitats, which was opposite my hypothesis that artificial lights around buildings would increase prey capture rate. It could be that the bulk of preys captured by *N. clavipes* are either not active at night or not attracted to artificial lights. This also probably occurred because the non-forest area is found on the edge of the tropical forest. It has been cleared of trees to erect a few buildings and prey could fly from the forest to the buildings rather than walking like males and kleptoparasites need to do.

N. clavipes females were larger in the forest than in the non-forest habitat, but there was no difference in web diameter. Although, spiders in the forest built webs along the trails, in more open spaces, they might have been more constrained by vegetation structure compared to spiders in the non-forest habitat where vegetation density was low. In one observation, there was a large spider occupying a web not much bigger than its body because the space between bamboo stalks was very narrow. Spiders occupying tight spots were not observed in the non-forest habitat. The smaller spider size in the non-forest habitat could be attributed to recolonization efforts by the spider and, specifically, the influx of younger spiders as they disperse after hatching. The spiders are typically

removed from the non-forest study area by the housekeeper, but this practice was discontinued at the beginning of the research period. The positive correlation between spider size and web diameter was expected because as spiders grow so does the size of the web (Foelix 2011). The strong correlation between spider size and web diameter was taken into account during the "Relationship among Variables" analyses by including only one of them as a predictor variable in a given analysis. In the analyses for median number of prey and kleptoparasite load, the web diameter was chosen as the predictor instead of spider size because larger webs have a larger trap area for prey and because it provides more space for kleptoparasites. In the analysis for median number of males, I included spider size because males usually copulate with mature females. Mature females are larger than juvenile females.

Finally, surprisingly because *N. clavipes* are not social spiders, about half of them were found in clusters, though clusters were larger in the forest habitat (up to four spiders with adjacent webs) than in the non-forest habitat (only up to two spiders clustered). Additionally, the spiders were arrayed in a pattern of different sizes, with each cluster having a small, medium, and large spider. The range of spider size rankings could be a strategy to reduce competition for males although there have been cases of cannibalism of the younger females by the older females (Wise 2006).

Web tenure

Web tenure in the forest locations was influenced by prey capture rate and inclusion in a cluster. Alternatively, kleptoparasite and male load did not relate to web tenure. Webs with more prey had shorter tenure, which was opposite my predictions, and clustered webs had longer tenure than singleton webs, which supported my predictions. The negative influence of prey on web tenure supports other studies (Rypstra 1981; Rittschof and Ruggles 2010). Spiders might be compelled to

abandon their web for some unknown reason, but starving spiders might not risk the dangers of venturing out of the safety of the web whereas spiders that have been adequately fed have better awareness of their surroundings and so feel safer in searching for a new site. To make up for nutrient deficiency, starving spiders delay their growth rate instead of searching for optimal conditions (Vollrath and Houston 1986) or they change the design of their web (Nakata 2007).

The longer web site tenure of clustered webs in the forest habitat cannot be ascribed to prey load because there were no differences in prey load between solitary and clustered webs. Since males and kleptoparasites did not have a significant effect on web tenure, the web tenure of clustered webs is probably increased by the safety benefits of clustering. A couple of the benefits include an early warning system and the selfish herd effect. Additionally, clustering in general had an interaction effect with spider size and web diameter on the presence of males and kleptoparasites. Males were more attracted to larger female spiders in clusters than in the solitary webs in the forest habitat. Larger female spiders are more likely to be reaching maturity, and clustering facilitates the migration between webs, and thus, different females (McCrate and Uetz 2010). The interaction between clustering and web diameter also culminated in an increase in kleptoparasite attraction to larger webs in clusters compared to solitary webs. The explanation is similar to the males' situation because clusters facilitate migration, and, as previously mentioned, larger webs have larger areas that provide more space for kleptoparasites. Since neither males nor kleptoparasites had an effect on web tenure, this means that the costs of having either of these organisms residing in the web are low and can be ignored. Kleptoparasites must not be important for the spider's decision over web tenure since their fitness is not compromised by competition for prey and they pose no danger. Spiders can overlook the presence of kleptoparasites and resource loss because they have the physical mechanisms to cope. In the case of males, the benefit of having more reproductive opportunities levels out the costs of harassment. One previous study found that

males affected the web tenure of mature females, but not that of immature females (Rittschof and Ruggles 2010). Although, it was sometimes difficult to definitively label a female as an adult when they were large and had opisthoma patterns close to the patterns of an adult, the majority of the spiders were indubitably juveniles. Therefore, males were not instituting copulation behaviors and the costs of harassment were not being felt by the female spider and therefore not influencing her web tenure decisions.

In the non-forest habitat, the results were different from the forest habitat. Prey load, kleptoparasite presence, male presence, nor inclusion in a cluster influenced *N. clavipes*' decision over web tenure. Rather, spider size was the strongest predicting factor— larger spiders had longer web tenure. Although mean spider size was smaller in the non-forest habitat, the range of sizes included a few large spiders. This range was enough to model the influence of spider size on web tenure. Larger spiders are older and are reaching the reproduction stage. Males often copulate successfully with mature females (Rittschof 2011). It logically follows that once spiders become gravid they are looking for a place to lay their eggs instead of changing their web site.

Relationship among Variables

Web diameter accounts for 20% of prey caught by *N. clavipes*. In both habitats, web diameter had a positive influence on prey load although the relationship was much stronger in the forest environment than in the non-forest environment. As expected, as spider size increased, or females reached maturity, there was an increase in presence of males in the forest habitat for spiders in a cluster and solitary spiders. However, inclusion in a cluster more strongly accounted for increase in male presence (34%). Although, the chances of a male arriving at colony versus a solitary web are equal (Meraz et al. 2011), as previously mentioned, clusters facilitate migration and males tend to arrive at webs where other males have been present (Meraz et al. 2011).

Lastly, kleptoparasites prefer larger webs because there is more space available, and cluster in the forest habitat accounts for kleptoparasite numbers slightly more than in the non-forest habitat. The reasoning is similar to the males in that clusters facilitate migration.

Conclusion

While previous studies have looked at one or a few variables that could affect web tenure, in this research, I studied the combined effects of multiple factors. This approach is helpful in trying to understand the complexity of different factors interacting with each other to determine a behavioral decision. Yet, analyses could benefit from exploring a wider range of possible factors influencing web tenure and taking into account variability in the environment such as sudden rainstorms. For example, I often observed clustering with heterospecific female spiders in the field and encountered literature describing this phenomenon. It would add an extra layer of understanding and possibly transform the results found from clustering with conspecific female spiders. The factors in this study were organismal interactions, so also including abiotic factors in the study would be ideal. The study area appeared fairly homogenous in terms of vegetation types, except between the forest and non-forest habitats, and humidity and temperature should have remained similar in the entire reservation. Therefore, the abiotic factor would quantify the amount of protection afforded by vegetation or buildings to the web. The results found that prey capture rate and cluster affected web tenure in forest habitats, but prey was unexpectedly negatively correlated with web tenure. This challenges the assumption that prey is a favorable predicting factor, and is in line with a previous study describing this negative relationship with web tenure (Rittschof and Ruggles 2010). In the non-forest habitat, spider size influenced web tenure which might be because larger spiders are reaching the egg production stage. The differences between the two habitats highlight the necessity of not generalizing results across different habitats despite spatial

proximity. Further experiments could identify other variables including abiotic ones to explore how *N. clavipes* decides the length of web tenure and how these variables interact with one another.

Acknowledgments

I would like to thank Dr. Elise Ferree for her ceaseless advice and for patiently supporting and guiding me. I am extremely grateful to Dr. Diane Thomson for her very thorough thesis comments as my second reader, to Dr. Donald McFarlane for his tropical rainforest tour guides, and to Warren Roberts for help with GIS and creating a professional-looking map. Finally, I thank the Norris Foundation and the W.M. Keck Science Department for the opportunity.

References

- Agnarsson, I., 2003. Spider webs as habitat patches -the distribution of kleptoparasites (*Argyrodes theridiidae*) among host webs (*Nephila*, Tetragnathidae). *Journal of Arachnology*. 31, 344-349.
- Blamires, S. J., Lee, Y., Chang, C., Lin, I., Chen, J., Lin, T. & Tso, I. 2010. Multiple structures interactively influence prey capture efficiency in spider orb webs. *Animal Behaviour*. 80, 947-953.
- Christenson, T., Brown, S., Wenzl, P., Hill, E., Goist, K., 1985. Mating behavior of the golden orb-weaving spider, *Nephila clavipes*. 1. female receptivity and male courtship. *Journal of Comparative Psychology*. 99, 160-166.
- Enders, F. 1977. Web-site selection by orb-web spiders, particularly *Argiope aurantia* lucas. *Animal Behaviour*. 25, 694.
- Foelix, R. F. 2011. *Biology of Spiders*. 3rd edn. New York, New York: Oxford University Press.
- Grostal, P., Walter, D., 1997. Kleptoparasites or commensals? effects of *Argyrodes antipodanus* (Araneae: Theridiidae) on *Nephila plumipes* (Araneae: Tetragnathidae). *Oecologia*. 111, 570-574.
- Grostal, P., Walter, D., 1999. Host specificity and distribution of the kleptobiotic spider *Argyrodes antipodanus* (Araneae, Theridiidae) on orb webs in Queensland, Australia. *Journal of Arachnology*. 27, 522-530.
- Heiling, A., Herberstein, M. 1999. The importance of being larger: intraspecific competition for prime web sites in orb-web spiders (Araneae, Araneidae). *Behaviour*, 136, 669-677.
- Hénaut, Y., Machkour-M'Rabet, S., 2010. Interspecific aggregation around the web of the orb spider *Nephila clavipes*: consequences for the web architecture of *Leucauge venusta*. *Ethology Ecology & Evolution*. 22, 203-209.
- Hénaut, Y., Machkour-M'Rabet, S., Winterton, P., Calmé, S., 2010. Insect attractions by webs of *Nephila clavipes* (Araneae: Nephilidae). *Journal of Arachnology*. 38, 135-138.
- Higgins, L., Buskirk, R., 1998. Spider-web kleptoparasites as a model for studying producer-consumer interactions. *Behavioral Ecology*. 9, 384-387.
- Hodge, M., Uetz, G. 1996. Foraging advantages of mixed-species association between solitary and colonial orb-weaving spiders. *Oecologia*. 107, 578-587.

- Hodge, M., Uetz, G. 1992. Antipredator benefits of single-species and mixed-species grouping by *Nephila clavipes* (L) (Araneae, Tetragnathidae). *Journal of Arachnology*. 20, 212-216.
- Kapoor, V., 2008. Effects of rainforest fragmentation and shade-coffee plantations on spider communities in the Western Ghats, India. *Journal of Insect Conservation*. 12, 53-68.
- Klokocovnik, V., Devetak, D., Orlacnik, M., 2012. Behavioral plasticity and variation in pit construction of antlion larvae in substrates with different particle sizes. *Ethology*. 118, 1102-1110.
- Krakauer, T., 1972. Thermal responses of the orb-weaving spider, *Nephila clavipes* (Araneae: Argiopidae). *American Midland Naturalist*. 88, 245-250.
- Larcher, S. F. & Wise, D. H., 1985. Experimental studies of the interactions between a web-invading spider and two host species. *Journal of Arachnology*. 13, 43-59.
- Leborgne, R., Cantarella, T., Pasquet, A., 1998. Colonial life versus solitary in *Cyrtophora citricola* (Araneae, Araneidae). *Insectes Sociaux*. 45, 125-134.
- LeGuelte, L., 1969. Learning in spiders. *American Zoologist*. 9, 145-152.
- McCrate, A. T. & Uetz, G. W., 2010. Kleptoparasites: a twofold cost of group living for the colonial spider, *Metepeira incrassata* (Araneae, Araneidae). *Behavioral Ecology and Sociobiology*. 64, 389-399.
- Meraz, L. C., Hénaut, Y., Elgar, M. A., 2012. Effects of male size and female dispersion on male mate-locating success in *Nephila clavipes*. *Journal of Ethology*. 30, 93-100.
- Mestre, L., Lubin, Y., 2011. Settling where the food is: prey abundance promotes colony formation and increases group size in a web-building spider. *Animal Behaviour*. 81, 741-748.
- Miyashita, T., 2001. Competition for a limited space in kleptoparasite *Arygrodus* spiders revealed by field experiments. *Population Ecology*. 43, 97-103.
- Miyashita, T., Shinkai, A., Chida, T., 1998. The effects of forest fragmentation on web spider communities in urban areas. *Biological Conservation*. 86, 357-364.
- Moore, C. W. 1977. Life-cycle, habitat and variation in selected web parameters in spider, *Nephila clavipes* Koch (Araneidae). *American Midland Naturalist*. 98, 95-108.
- Nakata, K. 2007. Prey detection without successful capture affects spider's orb-web building behaviour. *Naturwissenschaften*. 94, 853-857.
- Peters, P. J. 1970. Orb web construction: interaction of spider (*Araneus diadematus* Cl.) and thread configuration. *Animal Behaviour*. 18, 478-480.
- Pinkus-Rendón, M., Leon-Cortes, J., Ibarra-Nunez, G., 2006. Spider diversity in a tropical habitat gradient in Chiapas, Mexico. *Diversity and Distributions*. 12, 228-228.

- Rayor, L. S., Uetz, G. W., 1990. Trade-offs in foraging success and predation risk with spatial position in colonial spiders. *Behavioral Ecology and Sociobiology*. 27, 77–85.
- Rittschof, C. C., Ruggles, K. V., 2010. The complexity of site quality: multiple factors affect web tenure in an orb-web spider. *Animal Behaviour*. 79, 1147-1155.
- Rittschof, C. C., 2011. Mortality risk affects mating decisions in the spider *Nephila clavipes*. *Behavioral Ecology*. 22, 350–357.
- Robinson, M. H., Mirick, H., 1971. The predatory behavior of the golden-web spider *Nephila Clavipes* (Araneae: Araneidae). *Psyche*, 78, 123–139.
- Rosenzweig, M. 1991. Habitat selection and population interactions - the search for mechanism. *American Naturalist*. 137, S5-S28.
- Rypstra, A. L., 1981. The Effect of kleptoparasitism on prey consumption and web relocation in a Peruvian population of the spider *Nephila clavipes*. *Oikos*. 37, pp. 179-182.
- Rypstra, A. L., 1983. The importance of food and space in limiting web-spider densities; a test using field enclosures. *Oecologia*. 59, 312–316.
- Sherman, R. G., Pax, R. A., 1968. The heartbeat of the spider, *Geolycosa missouriensis*. *Comparative Biochemistry and Physiology*. 26, 529–534.
- Shochat, E., Stefanov, W., Whitehouse, M., Faeth, S., 2004. Urbanization and spider diversity: influences of human modification of habitat structure and productivity. *Ecological Applications*. 14, 268-280.
- Sih, A., Bell, A., Johnson, J. C., 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*. 19, 372-378.
- Townley, M. A., Tillinghast, E. K., 1988. Orb web recycling in *Araneus cavaticus* (Araneae, Araneidae) with an emphasis on the adhesive spiral component, gabamide. *American Arachnological Society*. 16, 303–319.
- Uetz, G. W., Hieber, C. S., 1994. Group size and predation risk in colonial web-building spiders: analysis of attack abatement mechanisms. *Behavioral Ecology*. 5, 326–333.
- Uetz, G. W., 1988. Group foraging in colonial web-building spiders - evidence for risk-sensitivity. *Behavioral Ecology and Sociobiology*. 22, 265-270.
- Uetz, G. W., 1989. The ricochet effect and prey capture in colonial spiders. *Oecologia*. 81, 154-159.
- Vollrath, F., 1980. Male body size and fitness in the web-building spider *Nephila clavipes*. *Zeitschrift Fur Tierpsychologie-Journal of Comparative Ethology*. 53, 61-78.
- Vollrath, F., Houston, A., 1986. Previous experience and site tenacity in the orb spider *Nephila* (Araneae, Araneidae). *Oecologia*. 70, 305–308.

Vulinec, K., 1990. Collective security: aggregation by insects as a defense. In: *Insect defenses: adaptive mechanisms and strategies of prey and predators* (Ed. by D. L. Evans & J. O. Schmidt), pp. 251. Suny Press.

Willey, M. B., Jackson, R. R., 1993. Olfactory cues from conspecifics inhibit the web-invasion behavior of web-invading araneophagic jumping spiders (Araneae: Salticidae). *Canadian Journal of Zoology*. 71, 1415–1420.

Wise, D. H., 2006. Cannibalism, food limitation, intraspecific competition, and the regulation of spider populations. *Annual Review of Entomology*. 51, 441–465.

Yip, E. C., Powers, K. S., Avilés, L., 2008. Cooperative capture of large prey solves sealing challenge faced by spider societies. *Proceedings of the National Academy of Sciences of the United States of America*. 105, 11818–11822.