

# Patch Richness Affecting Patch Selection of *Pityophantes*

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## Abstract

We observed spiders of the family *Linyphiidae* and genus *Pityohyphantes* in two different microhabitats at the University of Michigan Biological Station near Pellston, Michigan. The purpose of this study was to explore the effects of prey distribution on spider foraging behavior in the two microhabitats. The microhabitats were composed of a temperate forest woodland understory and a shoreline habitat along Douglas Lake. Microhabitat richness was measured by observing potential prey abundance, number of prey captured on sheet webs, and biomass of captured prey in both microhabitats. The shoreline microhabitat was found to have a higher abundance of potential prey of the two areas under study. However, the woodland understory was observed to have a higher average prey capture count and biomass per web. Unfortunately, our results conflicted depending on what criteria was used. Though we could not definitively say which was the richer patch, we did find variability in patch richness. Despite the variability in patch richness, an equal distribution of sheet webs was found between the two microhabitats. These results suggest that factors other than prey distribution affect patch selection. Although outside the scope of our study, tradeoffs such as competition or predation likely result in *Pityohyphantes* spiders preferring a microhabitat with less potential prey.

## Introduction

An organism's life history strategy strongly affects a variety of its behavioral traits. In short-lived semelparous organisms, sufficient feeding and the ability to reproduce determine much of their fitness. Both feeding and reproduction greatly depend on the foraging strategy of the organism. According to the optimal foraging theory, a predator's foraging strategy depends greatly on the availability of vital resources, such as prey. Furthermore, optimized foraging strategy maximizes net energy gained from prey while minimizing energy spent on the search and handling time of prey. For web-weaving spiders, the amount of time pursuing prey can be neglected (Cooper & Anderson, 2006). Handling time of prey, however, may become an important variable since spiders generally take longer to subdue and consume larger prey. Optimal foraging theory also depends upon an organism's use of generalist or specialist foraging strategies (Beals 1999). Most web building spiders are considered generalist foragers that prey on a wide range of arthropods. Typically a spider will consume any type of prey that becomes

entrapped in the web and that the spider is capable of consuming (Riechert 1999). This makes web location key to a spider's foraging strategy.

As a spider creates a web, many factors affect the location of the web. The non-uniform distribution of vital resources in the habitat cause patches of varying resource richness in the greater habitat (Levin and Paine 1974, Wiens 1976 in Rotenberry 1998). Patch selection is a key aspect affecting the relative fitness of spiders in a habitat since an increase in prey capture is correlated with a larger body size, which increases fecundity (Edwards 1980). Patch selection depends on both patch richness and the risk of perturbation. In general, an animal will only hunt in a particular patch if it perceives it is more profitable than surrounding areas (Daigle 2004). However, if energy spent on obtaining the prey outweighs the energy gained from the prey due to perturbation in one patch, a spider will often emigrate to a new patch with lower prey availability if the new area has less perturbation in an attempt to minimize energy spent in web maintenance (Leclerc 1991). Other factors that can influence habitat selection include exposure to predators, inter- and intraspecific competition and cover (Rotenberry & Wiens, 1998). Due to an organism's inability to accurately assess environmental variables within a habitat, it will make safer, risk averse decisions. Spiders choose habitats with a more consistent prey encounter rate over a habitat that alternates between extremes of high and low prey densities (Riechert 1999).

Predation rates on a spider within a patch can adversely affect its occupation or use of that particular patch. Spiders in patches where predators are prevalent have shown suboptimal foraging behavior in order to decrease their risk of predation (Leclerc 1991). For example, in patches where there are fewer predators, orb web spiders may position

themselves at the hub, or middle, of the web when foraging. In such a patch, the decreased response time due to being in the center of the web outweighs the risk of predation since there are few predators. However, in areas where the risk of predation is high, the spiders were found to reside at the edges of webs when foraging. This puts the spiders at less risk to predation but also increases response time, causing them to be less efficient hunters (Bruce & Herbstein, 2006). Although we are studying sheet web weavers, a different family of spiders, we noticed during our observations in the field that *Pityohyphantes* exhibited both patterns of positioning on their webs, suggesting they may respond to predation pressure in a similar manner.

As population density increases in a given habitat, foraging efficiency is likely to decrease due to increased intraspecific competition with more individuals vying for the same resources. As a population climbs towards a habitat's carrying capacity individuals are forced to occupy suboptimal microhabitats since more optimal microhabitats have already been occupied (Svardson 1949). In our study, although one microhabitat may be more profitable, the spider population still occupies a larger range due to intraspecific competition.

Our study looks at the relative success rate of prey capture within the subfamily *Linyphiinae* and genus *Pityohyphantes* in two different microhabitats of northern Michigan. The study attempts to understand the relationship between potential prey availability, prey capture count, and captured prey biomass across two microhabitats. For the purpose of our study we designate the entire woodland under study as the habitat. The shoreline and woodland understory are defined as two microhabitats that could potentially be considered two different patches if a difference in resources, such as prey

availability, is found. If one microhabitat has a higher abundance of potential prey, a higher prey capture count, and a higher prey biomass we assume that this patch is a higher quality area and thus a more desirable location for *Pityohyphantes* to build their webs. Accordingly, we ask:

1. Does the relative abundance of prey differ in the two microhabitats under observation?
2. Does the relative prey capture count in webs differ in the two microhabitats under observation?
3. Does the relative captured prey biomass in webs differ in the two microhabitats under observation?
4. If a difference in prey abundance, prey capture count, or captured prey biomass is found between the two microhabitats, are more spiders foraging in the richer patch?

#### Materials and Methods

##### *Experimental Organism*

Sheet web spiders of the subfamily *Linyphiinae* and the genus *Pityohyphantes*, build nearly horizontal webs to catch prey. The webs are composed of a central horizontal sheet that includes support strands of silk extending to the surrounding vegetation in order to keep the web intact. Like others in the *Linyphiinae* subfamily, spiders in the *Pityohyphantes* genus are generalist predators that utilize a sit-and-wait hunting strategy. The spider creates a web to catch prey, and once a prey is caught, the spider feels the vibrations of the struggling insect. The spider then injects the insect with venom and/or wraps the prey in silk to ensure capture (*Encyclopedia of Insects* 1071). Though identification of species was not carried out due to logistical constraints, the spiders observed in our study were generally brown in color, approximately two centimeters in length, and had a large, elongated abdomen. The selected spiders perched on juvenile tree branches or other understory plant matter such as fallen trees. In the

inland microhabitat, the spiders notably constructed their webs on young conifers such as white pine trees, while the shoreline subset constructed their webs on hanging vines and on dead trees, both standing and fallen.

### *The Effect of Microhabitat on Potential Prey Abundance*

To determine the effect of microhabitat on available prey, we set up five transparencies covered with adhesive Tanglefoot in each microhabitat. These “sticky papers” were hanged from trees located along each transect and spaced twenty meters apart. They were used to catch aerial insects from each of the microhabitats to measure potential prey abundance. At the end of a two week time period, we collected the sticky papers and counted the total amount of insects caught in each location (Figure 1).

To statistically analyze the data from both locations, we carried out a t-test on the program “SPSS” to compare the mean prey count caught by sticky paper in both microhabitats.

### *The Effect of Microhabitat on Average Prey Capture Count*

Since abundance alone indicates only what is potentially available to the spiders, we measured the actual prey capture count to obtain the number of prey the web catches. To determine if there is a difference in prey capture count in the wood and shoreline microhabitats, we set up a 100 meter transect divided into ten meter intervals along Grapevine Trail on the University of Michigan Biological Station property. We measured the distance from the center of the path to the Douglas Lake shoreline at each ten meter interval. That measurement was then used to measure an equidistant line from

the center of the path to the inland woods. Webs were found within a 2x2 meter box at corresponding points along the shoreline and in the woodland (Figure 2). The chosen webs were each at least two meters apart to ensure independence from each other. Also, for each web chosen we noted the approximate web surface area. Eleven webs were marked and observed in the woods. Seven webs were marked and observed along the shoreline (Figure 3). Only webs 0.25 meters to 2.00 meters above the ground were sampled to exclude other families of spiders such as of Tunnel-web weavers, which build similar webs in leaf litter.

Each spider was removed from its respective web in order to remove confounding variables caused by behavioral aspects of the spider. For example, the spider may eat and/or discard what was caught in the web or alter the web quality. Removing the spider eliminates many variables and assumptions that would otherwise alter our data. Our web observations took place over a four day period. We returned to the webs every twenty four hours at approximately 16:00 to count the number of prey caught in each web.

To statistically analyze the data from both locations, we carried out a t-test on the program "SPSS" to compare the average capture count caught by both inland and shore webs.

### *The Effect of Microhabitat on Captured Prey Biomass*

Another measure of patch richness is the biomass of the captured prey obtained from each web sample. The biomass indicates how much energy the spiders could obtain. At the end of our four day study period, we removed the total prey caught in each web using tweezers. Otherwise, prey removal after each twenty-four hour period would cause

damage to the web altering our data. We massed the prey from each web using a Mettler AE-240 microscale.

To statistically analyze the data from both locations, we carried out a t-test on the program “SPSS” to compare the captured prey mean biomass caught by both inland and shore webs.

### *Relative Abundance of Spiders*

In our study, resource availability in the two microhabitats is indicated by prey abundance, captured prey biomass, and prey capture count. To determine if there is a relationship between resource availability and the abundance of sheet web weavers, we counted the number of sheet webs in both microhabitats. On the shoreline, we counted webs falling within two meters from the shoreline along the 100 meter transect. Along the woodland transect, we counted all sheet webs along the 100 meter transect limiting webs found within one meter on both sides of the transect. Abundance of spiders is indicated by the number of webs found in each microhabitat. In areas with a larger abundance of sheet webs, it is expected that the abundance of sheet web weavers should also be greater.

To statistically analyze the data, we carried out a  $X^2$  test to compare the relative abundance of webs found in both microhabitats.





## Results

Before analyzing data relating to any of our hypotheses, we first considered the consistency among each microhabitat. For seven corresponding webs on the shoreline and the woodland, we used an ANOVA and Post Hoc test comparing evenness of microhabitats based on prey biomass ( $p = 0.839$ ) (Figure 4). This analysis suggests that the two microhabitats are consistent to continue our study.

### *Potential Prey Abundance*

At the end of our four day study, the sticky papers were collected. The sticky paper placed at the sixty meter location along the shoreline could not be found after the two-week time period. Therefore, at the sixty meter location in the woods, the corresponding sticky paper data was not included in the analysis. A total of 825 insects were counted in the shore microhabitat; a total of 455 insects were counted in the woodland microhabitat. Our t-test indicates a statistically significant difference in potential prey abundance between the two microhabitats. The shoreline microhabitat has a significantly higher potential prey abundance (Levene's test, equal variances assumed sig. = 0.962,  $p = 0.043$ ) (Figure 5).

### *Average Prey Capture Counts*

For the eighteen sampled webs, we compared the average prey capture counts between each microhabitat. Equal variance of average prey capture counts in the two microhabitats can be assumed (Levene's test,  $p = 0.074$ ). It was found that the mean prey capture count over the four days was significantly different between the two

microhabitats, and that the webs in the woodland understory captured a statistically larger prey count (t-test,  $p = 0.032$ ) (Figure 6).

#### *Captured Prey Biomass*

For the eighteen sampled webs, we compared the mean biomass of the captured prey between each microhabitat. Equal variance of biomass captured per web in the two microhabitats cannot be assumed (Levene's test,  $p = 0.002$ ). It was found that the mean biomass captured per web over the four days was significantly different between the two microhabitats, and that the webs in the woodland understory captured a greater biomass of prey (t-test,  $p = 0.004$ ). On average, woodland webs captured an average of 0.0016 grams of prey while shoreline webs captured only an average of 0.000229 grams of prey (Figure 7).

#### *Average Prey Capture Counts vs. Web Surface Area*

We graphed the variation in prey capture count in each microhabitat for each day of the study (Figure 8 and 9). In general, we found more variation in the woodland. The average prey capture counts were found to be greater in the woodland microhabitat. In the woodland microhabitat, as the web surface area increases, the average prey capture count increases as well. However, in the shoreline microhabitat, as the web surface increases, the average prey count decreases. We ran a regression test to show correlation between average number of prey capture and web surface area for each microhabitat. The woodland webs' regression has a linear  $R^2$  value of 0.213, and the shoreline webs' regression has a linear  $R^2$  value of 0.033 (Figure 10). The higher  $R^2$  value shows more

correlation between webs. P-values for woodland and shoreline are 0.696 and 0.153 respectively, showing no significant relationship between average capture count and web size in both microhabitats.

#### *Captured Prey Biomass vs. Web Surface Area*

A regression was used to evaluate captured prey biomass versus web surface area for both microhabitats. The woodland webs' regression has a linear  $R^2$  value of 0.102, and the shoreline webs' regression has a linear  $R^2$  value of 0.021 (Figure 11). The higher  $R^2$  value shows more correlation between webs. P-values for woodland and shoreline are 0.338 and 0.757 respectively, showing no significant relationship between captured prey biomass and web size in both microhabitats.

#### *Spider-Web Abundance in the Two Microhabitats*

Fifty-four webs were found in the shoreline microhabitat; seventy webs were found in the woodland understory microhabitat. We performed a  $X^2$  test to determine the significance of web abundance in both microhabitats. The  $X^2$  value equals 2.064 resulting in a p-value greater than 0.05. This suggests no significant difference in web abundance between the two microhabitats.

#### *Reinhabited Webs vs. Vacant Webs*

Throughout our study, we noticed new spiders reinhabiting the vacant webs which we had previously removed the initial spider. Nine out of the total eighteen webs were reinhabited by a new spider at some point in our study. To determine if these new spiders

had any effect on prey capture counts or prey biomass, we performed t-tests comparing the means of reinhabited webs and vacant webs. The t-test comparing average prey capture counts suggests no significant difference ( $p = 0.212$ ) (Figure 12). The t-test comparing means of prey biomass suggests no significant difference ( $p = 0.390$ ) (Figure 13).

## Discussion

At the outset of our study we expected variability in resource richness between the shoreline and woodland microhabitats. Specifically, we expected the shoreline to be a richer patch based on all three criteria: 1) potential prey abundance 2) captured prey count on the webs 3) captured prey biomass. As a result, we expected the spiders to prefer the shoreline patch.

Depending on which criteria was used, however, our results indicated an inconsistent ranking of the microhabitats' relative resource richness. All results point to a variability in patch richness, but we cannot definitively rank one patch richer than the other based on a single criterion. If we consider potential prey abundance more reliable criteria for patch richness, we conclude that the shoreline is a richer patch since sticky paper along the shoreline caught a significantly higher amount of potential prey than the woodland sticky paper. Conversely, if captured prey count and biomass were considered more accurate indicators of patch richness, we would conclude that the woodland is the richer patch since the woodland webs caught a greater number and prey biomass.

Due to logistical constraints, none of the criteria used in the study was perfectly ideal. Potential prey abundance may not have been an accurate indicator of patch richness for several reasons. By its very nature, a simple prey count from the sticky paper will not take into account size or mass of prey, which are closer estimates of energy gained from prey. Moreover, sticky paper may catch prey that webs cannot, or vice versa, so prey count from sticky paper may not accurately estimate what the webs catch. On the other hand, a count and biomass measure of prey caught in the webs may not have been ideal criteria for patch richness. This could be due to the fact that without the spiders, the

webs could have caught a non-representative amount of prey. Also, without the spiders present in our study, prey may have fallen off of the web due to wind or other abiotic factors that normally would have been secured by the spider. In our study, we did not weigh any one criterion greater than the other so we are unable to definitively say which was the richer patch. Based on our group's observations, we think that prey biomass would be the most sufficient criteria for calculating patch richness. We chose this option because the prey biomass was collected directly off the web. There would be no discrepancy in what could be caught and what was actually caught. Future studies would profit from a more comprehensive measure of patch richness in order to avoid such conflicting results.

Assuming that the web count is an accurate representation of the number of spiders in each patch, spiders did not show significant preference to the richer patch. In any case, an equal distribution of spiders could be due to several reasons. First, it could be a result of intraspecific competition. As the richer patch approached carrying capacity, the logistic population growth curve explains that crowding stresses on limiting resources such as available prey and space for webs would cause stabilized population growth (Kingsland 1982). Furthermore, the marginal value theorem of the Optimal Foraging Theory explains that a forager will only remain in a patch as long as it is more profitable for that organism to remain than to emigrate to another patch. Profitability is based on reward gained from prey versus required search, and handling time for that particular prey (MacArthur and Pianka 1966). As the richer patch became more crowded, intraspecific competition may decrease patch profitability resulting in forager emigration from the richer patch to the less rich patch in order to avoid crowding factors.

Second, density-dependent predation on the spiders may also explain the trend for equal spider distribution in the two patches, despite variability in patch richness. As the spider population increased in the richer patch, predators of spiders such as birds, amphibians or other animals may have found it more profitable to prey on spiders in this patch (Sih 1984). Consequentially, increased predation would regulate spider population in the richer patch and would also result in increased emigration to a new, more profitable patch.

### *Assumptions & Errors*

Despite our best efforts to limit confounding variables, there were obviously shortcomings to our experimental design. In order to proceed with our experiment, we had to make several key assumptions involving both our organism under study and our experimental approach. When collecting and counting prey caught in the webs, we assumed that all prey in the web would be consumed if the spider was present. This ignores both the spider's ability to subdue prey and also some assumptions of Optimal Foraging Theory, which indicates an organism will eat only the prey that best maximize its energy obtained. Unfortunately, it was not possible for us to explore the prey preference of *Pityohyphantes* over our study period due to the intense observation periods that this would entail. When sampling the distribution of webs in both of our study patches we had to assume that each web tallied was constructed by one spider and was not an old web that was no longer in use. However, we did not include damaged webs due to the fact that spiders will either ingest all or some of the silk used in the web when abandoning it (*Encyclopedia of Insects* 2003). Furthermore, we were not able to locate all spiders on webs tallied and thus were forced to assume that all of the sheet webs were



constructed by our study organism, *Pityohyphantes*. Lastly, due to our inability to accurately identify a particular species of *Pityohyphantes*, we assumed that all species within that genus have similar foraging strategies.

Some errors added constraints to our study. Some of these errors were simply outside the scope of our study and can be improved on in future studies. A larger study size would have been helpful in establishing stronger trends and allowed us to report our conclusion with more confidence. One of the constraints that restricted us to such a small sample size was the difficulty of locating spiders to remove from webs, particularly in the shoreline patch. As previously noted we were only able to locate 7 webs with spiders on them in the shoreline patch compared to 11 webs in the woodland patch. *Pityohyphantes* spent less time poised under its web and concealed itself more along the shoreline. Obviously, this is one of the problems that was outside of our control due to the correlative approach of our study. Nonetheless, this is a possible indicator that spiders alter their behavior in the face of biotic or abiotic stresses. Another factor that we had difficulty accounting for was the effectiveness of a web without the spider. It is very likely that the capture rate of webs decreased in both patches since the spider was not present to subdue prey attempting to escape. One study, previously mentioned, explains the strong effect that the spider has on prey capture. Even the spider's position on the web, whether it is poised on the fringe or hub of the web, affects foraging efficiency (Bruce & Herbstein).

Future research should consider our study's constraints when carrying out experiments to learn more about the topic of foraging behavior in sheet web spiders. As our experiment progressed and our knowledge of our area of study increased we began to

notice more areas of study that were outside the scope of our study but that were important to better understanding optimal foraging for *Pityohyphantes* spiders and other organisms. Future studies should consider several issues. First, manipulative experiments should be used to further consider the effect of predation on a spider's decision to inhabit patches of different profitability. Previous research has explored this relationship finding evidence that foragers consistently trade food for safety when predation and foraging conflict within a patch (Holbrook & Schmitt 1988, Sih 1980). However, this study does not explore the question of the effects of predation on patch selection and, in fact, many experiments involving predation and foraging fail to address this issue. This raises the question of what size patch can be considered relevant for such a small organism, which would require tests on a spider's dispersal abilities. Ultimately, patch selection is based on many factors, only a fraction of which were included in the scope of our study.

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**Figure 1. Sticky Paper (SP)  
Locations**

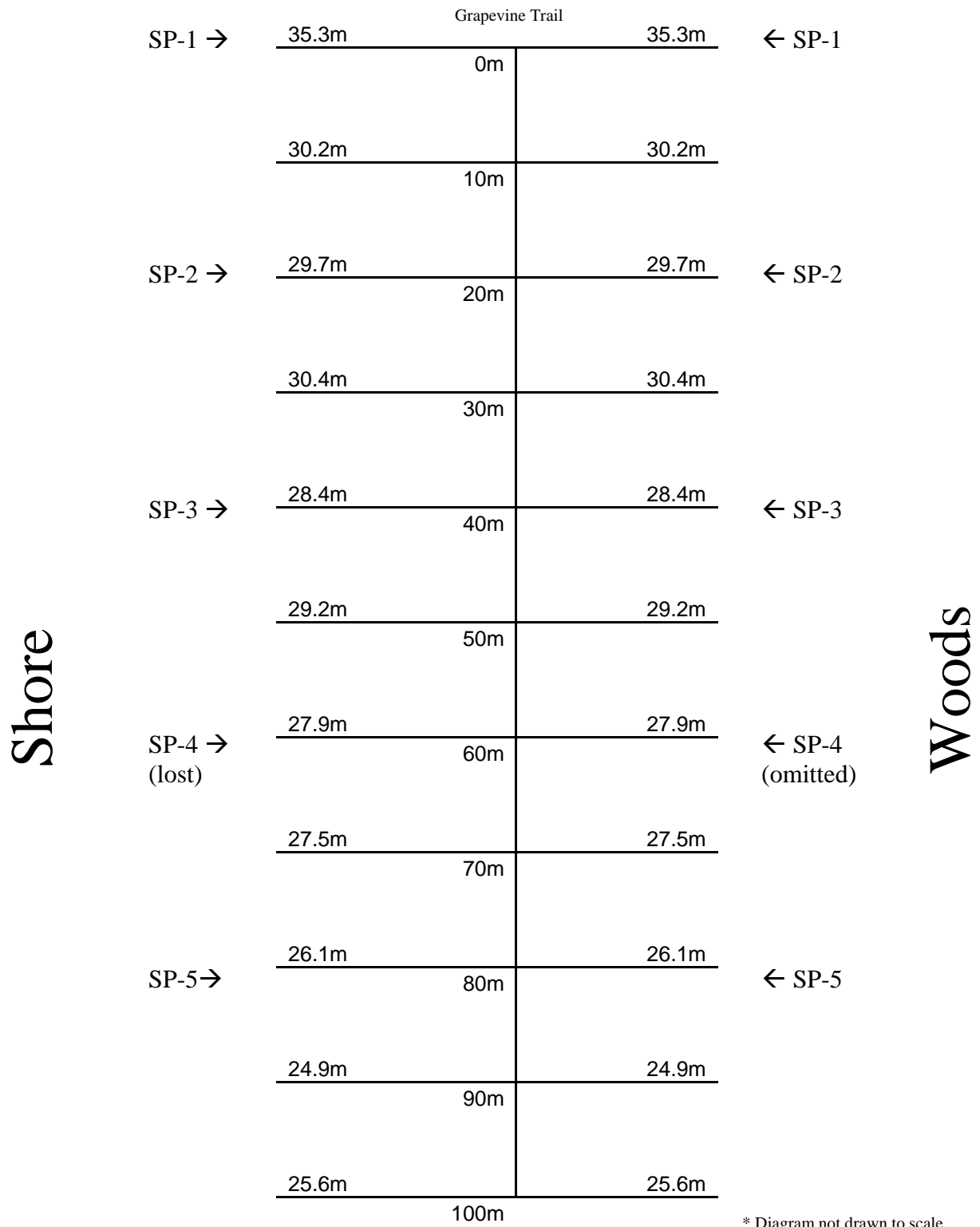
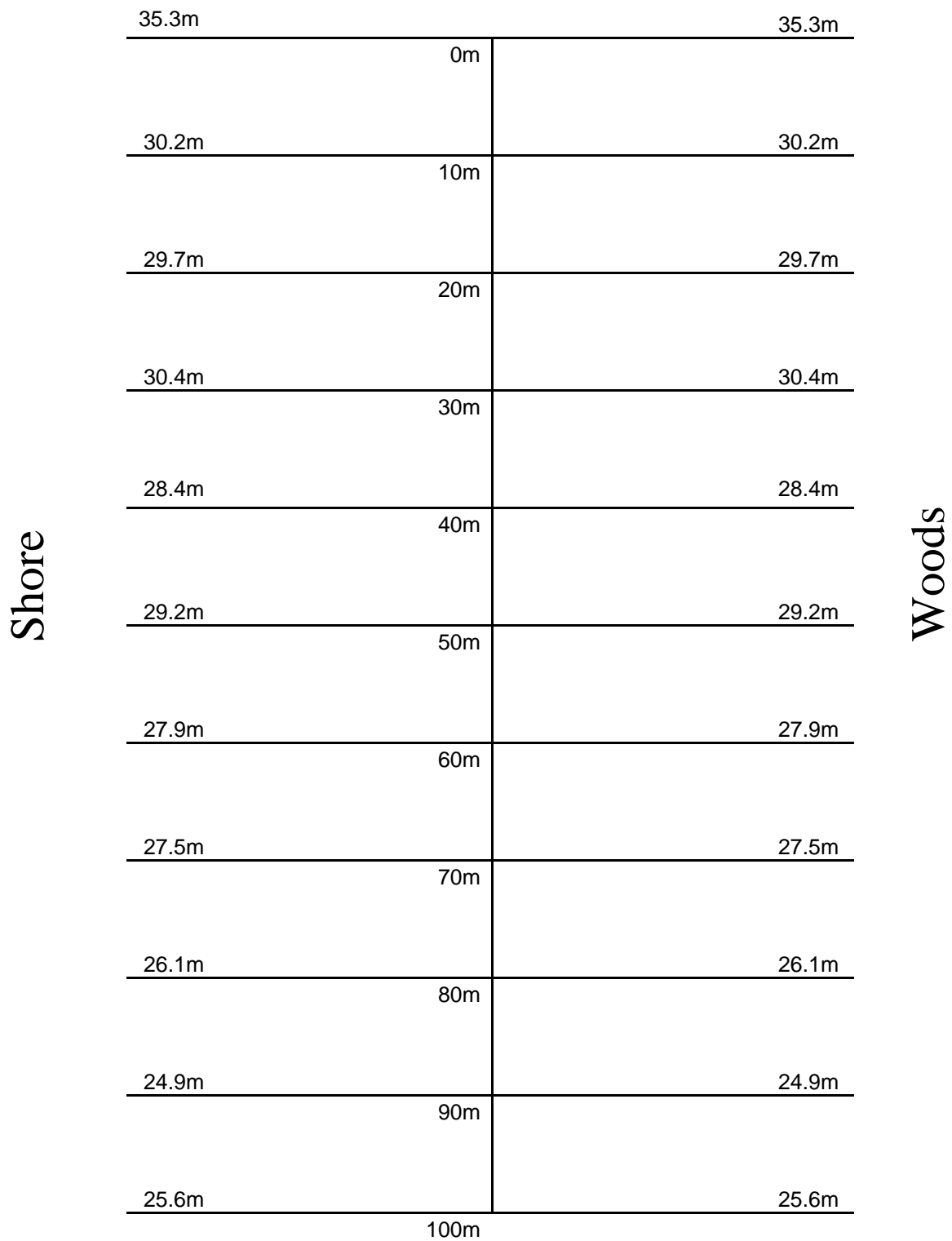
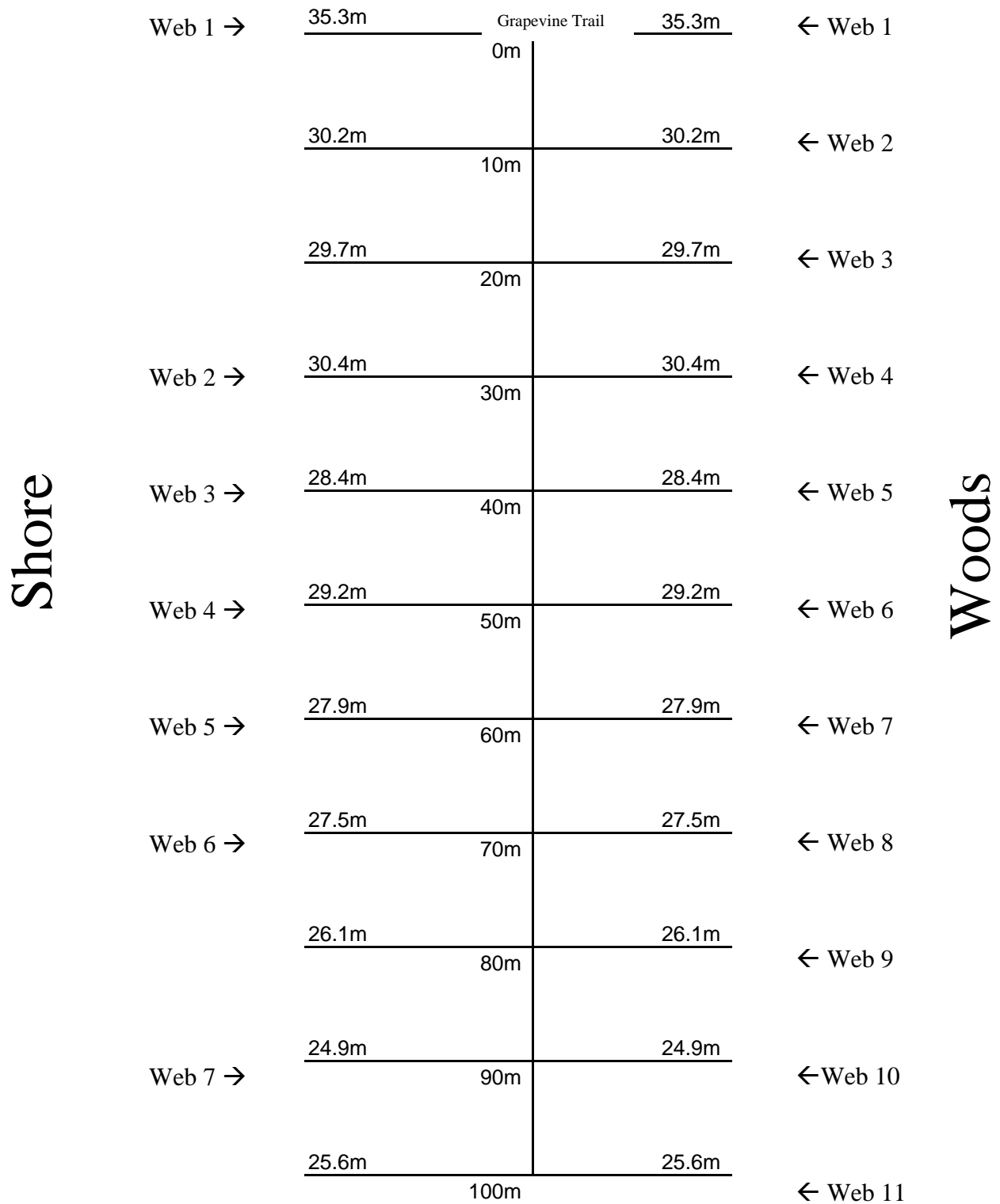


Figure 2. 100 Meter Transect Along Grapevine Trail



\*Diagram not drawn to scale

Figure 3. **Web Locations**



\*Diagram not drawn to scale

Figure 4.

**ANOVA**

Biomass

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	.000	6	.000	.429	<b>.839</b>
Within Groups	.000	7	.000		
Total	.000	13			

Figure 5.

		Levene's Test for Equality of Variances		t-test for Equality of Means						
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	95% Confidence Interval of the Difference	
								Lower	Upper	
Sticky Paper	Equal variances assumed	.002	.962	-2.562	6	<b>.043</b>	-92.500	36.108	-180.853	-4.147
	Equal variances not assumed			-2.562	5.915	.043	-92.500	36.108	-181.162	-3.838

Independent Samples Test

Figure 6.

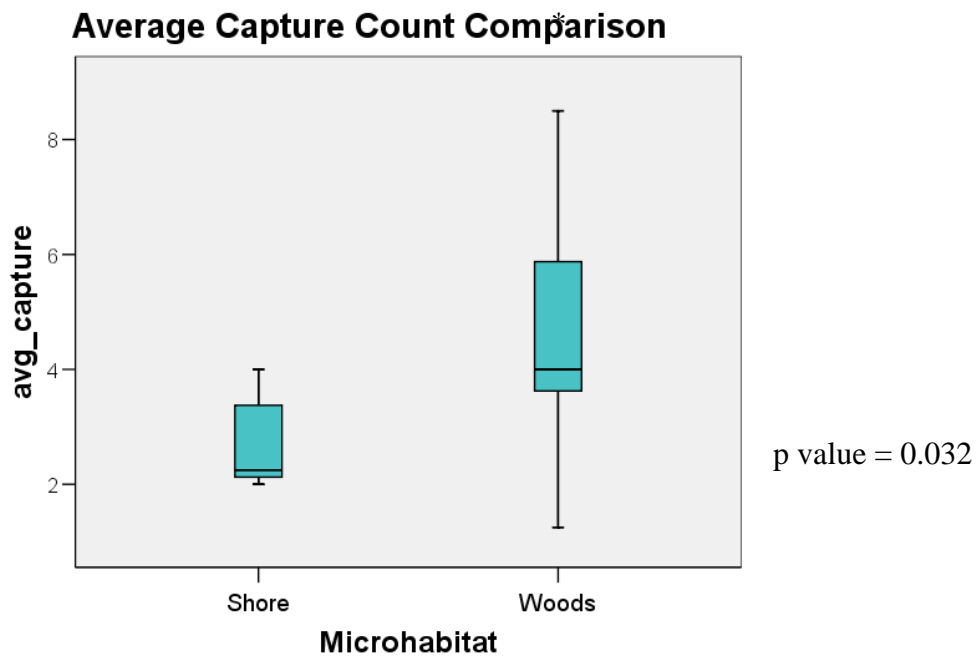


Figure 7.

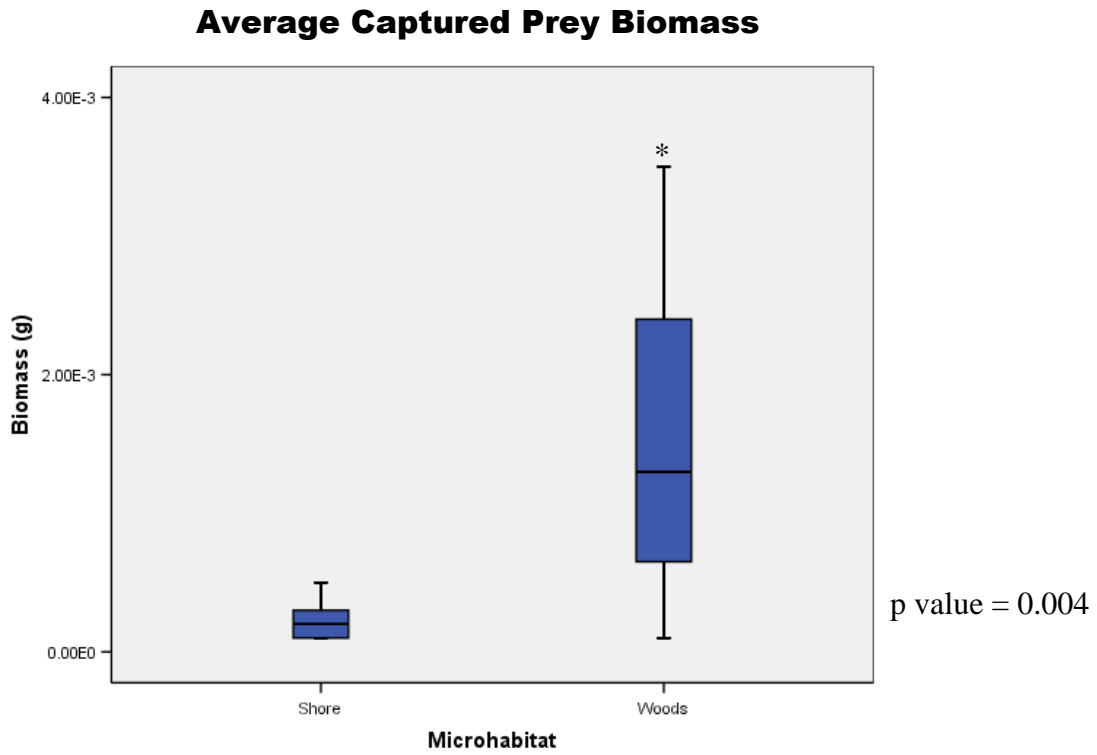


Figure 8.

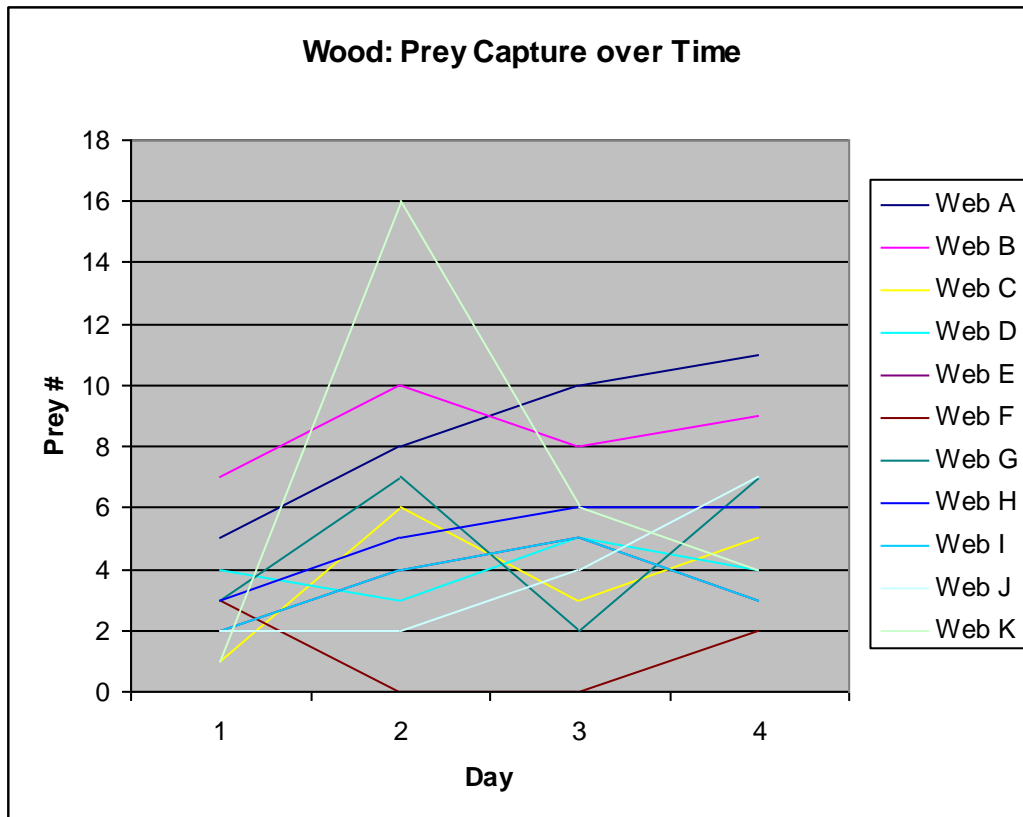




Figure 9.

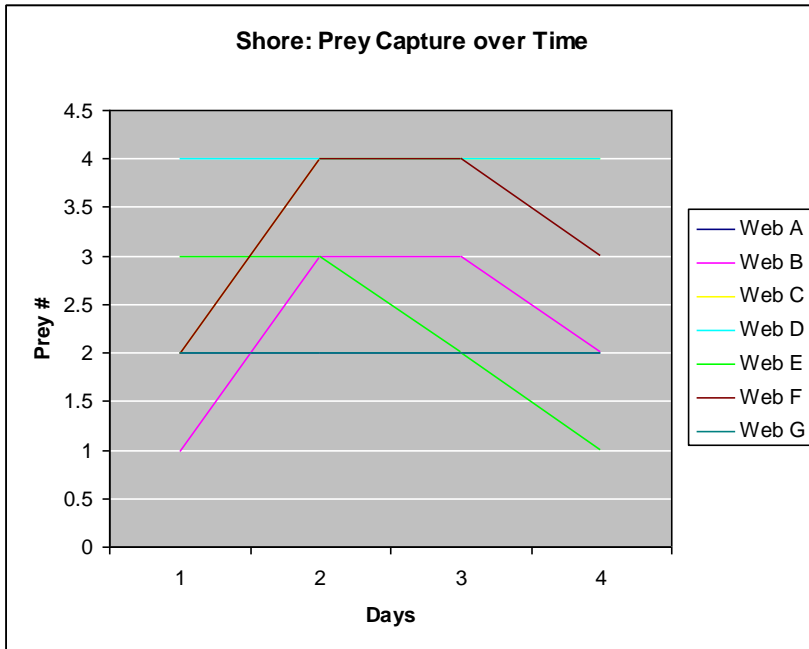


Figure 10.

### Regression: Average Prey Capture vs. Web Size

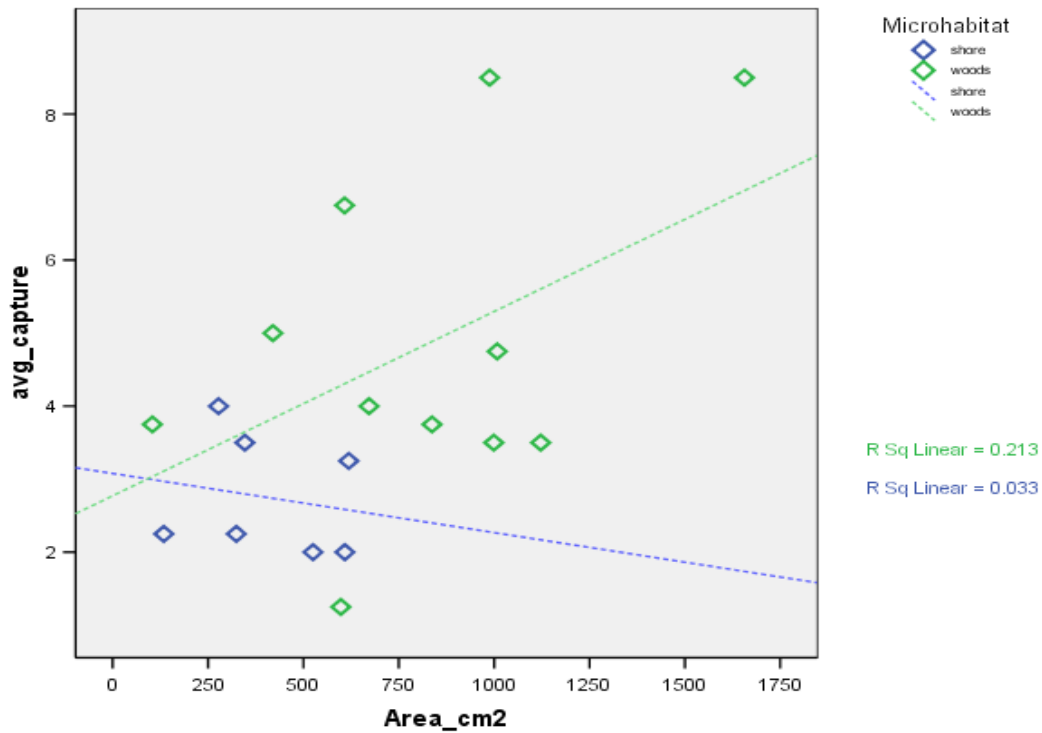


Figure 11.

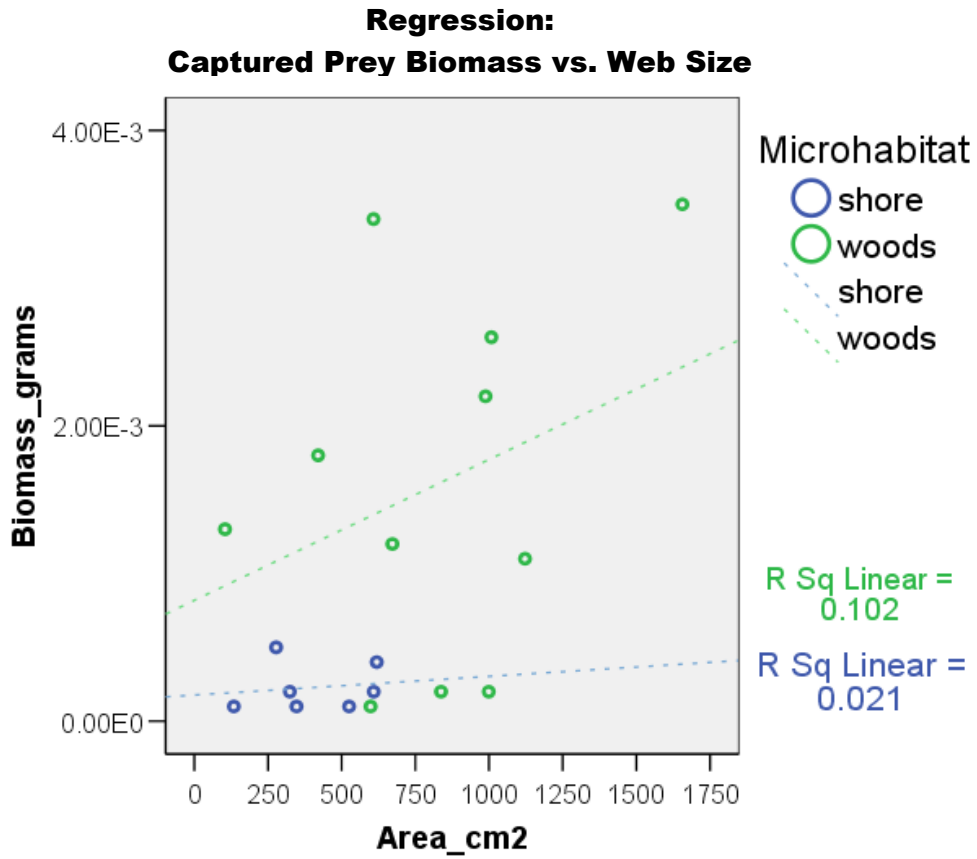


Figure 12.

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means						
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	95% Confidence Interval of the Difference	
									Lower	Upper
Average capture	Equal variances assumed	1.156	.299	1.303	15	<b>.212</b>	1.28125	.98334	-.81468	3.37718
	Equal variances not assumed			1.337	13.764	.203	1.28125	.95807	-.77690	3.33940

Figure 13.

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means					95% Confidence Interval of the Difference	
		F	Sig.	t	df	Sig. (2-tailed)	Mean Difference	Std. Error Difference	Lower	Upper
Prey Biomass	Equal variances assumed	1.352	.262	-.884	16	<b>.390</b>	-.0004888	.00055332	-.001661	.0006841
	Equal variances not assumed			-.884	15.317	.391	-.0004888	.00055332	-.001666	.0006883