Biodiversity Survey of Spiders at PCCI and Study of Sexual Size Dimorphism in Order Araneae

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Undergraduate Research Grants for the Environment Report

31 October 2014

ABSTRACT

From June to August of 2014, the biodiversity of spiders (Order Araneae) and the occurrence of sexual size dimorphism within Order Araneae was investigated at Pierce Cedar Creek Institute near Hastings, MI. Forty species of spider from thirteen families were identified. Many PCCI species favored environments with high humidity levels. These species were likely observed due to the 255 acres of wetland habitats, and 13 acres of open water that make up almost half of PCCI property, as well as the high amount of precipitation and humidity that was experienced during the 2014 summer. The most common spiders encountered were from Family Araneidae (orbweavers) and Family Lycosidae (wolf spiders). The two most remarkable species identified were the Northern Black Widow, *Latrodectus variolus*, and the uncommon wolf spider, *Lycosa modesta.* We sought to test a link between predation strategy and SSD within Order Araneae, but did not find data fully supporting our prediction – that SSD was related to difference in male and female predaceous foraging strategies. We concluded that further investigation is required to better understand the evolution of SSD within Order Araneae.

INTRODUCTION

Spiders (Class Arachnida, Order Araneae) comprise a diverse and often underappreciated arthropod group comprising nearly 4,000 species in North America alone, with an evolutionary history greater than 400 million years (Borror and DeLong 2005). All spiders are predaceous and play a well-known role in controlling the abundance of insects and other arthropods—including other spiders. They also serve as prey for a number of invertebrate and vertebrate animals.

Beyond this, spiders also exhibit some of the most amazing examples of sexual size dimorphism (SSD) in terrestrial animals (Foellmer and Moya-Larano 2007). Sexual dimorphism (SSD) is the distinct difference in appearance (size, color, etc.) between sexes of the same species. Sexual dimorphism in spiders can be observed in size, as well as color and decoration between males and females. SSD is a result of natural and sexual selection. When natural selection is weak and genetic diversity is high, joint evolution of sexually dimorphic sexes will result in a favorable phenotype for each sex (Lande, 1980).

For example, in several families of orb-weaving Orbiculariae spiders (Araneidae and Tetragnathidae) females may weigh several hundred times as much as males at maturity (Andersson 1994; Head 1995). Although SSD has been a well-documented phenomenon even from Darwin's time (Darwin 1871 *in* Foellmer and Moya-Larano 2007), the possible reasons for the size disparity between males and females is still poorly understood and no hypothesize provides a full and satisfactory explanation of SSD in spiders. However, even the often proposed "increased fecundity" of large females as a possible selective advantage for enormous females must be balanced by the fact that greater size presents greater visibility to predation as well (Foellmer and Moya-Larano 2005). Furthermore, we do not know if an increase in fecundity actually translates into a greater number of viable offspring (Corcobado, 2010).

There are a number of other possible explanations for male-biased dwarfism and female-biased gigantism. For example, "optimal climbing speed" in orb-weaving males has recently been suggested as an evolutionary selective pressure causing male dwarfism (Moya-Larano et al 2009). This hypothesis (derived from the so-called "gravity hypothesis") proposes that extreme SSD has evolved in spiders because smaller males *may* have a mating or survival advantage: they can climb (webs and other structures) with greater speed and therefore reach females faster. However, this hypothesis does not explain why apparent *reversals* in SSD have occurred within this same clade. Cladistic methods have been used in an attempt to "disentangle the contribution of many factors to evolutionary pattern by viewing them in a historical context" to establish the independence, distinctiveness, and possible sequence of evolutionary events (Nylin and Wedell, 1994), but without much success.

Other proposals suggest that small males avoid cannibalistic females because they are not seen as prey (Elgar and Fahey, 1996), or that male-to male-competition over access to females is relaxed when males are small (Ghiselin, 1974). It may be that specific patterns of selection vary from species to species even within a family, and thus each is the unique result of selective pressures over the course of their anagenetic evolution. Thus the evolution of extreme SSD has remained problematic and unresolved since the time of Darwin (Coddington *et al.* 1997). Whether or not the SSD is due to female gigantism or male dwarfism is still not known with certainty but it is known that spiders are the only terrestrial animal taxon in which extreme SSD is relatively common (Andersson, 1994).

"It is now widely agreed that fecundity selection in females and sexual selection in males provide fuel for some of the major evolutionary forces selecting for SSD, at least in invertebrates such as spiders (Andersson, 1994)." Several recent publications (e.g., reviewed by Moya-Larano, 2007) have presented a number of "differential equilibriuim models" for the evolution of SSD (Blanckenhorn 2000). However, these models seem to fall short of evolutionary explanation because most studies, especially in vertebrates tend to be taxon specific (Fairbairn 1997) and pertain mostly to vertebrates, *not* invertebrates such as the Araneae.

There is no over-arching hypothesis at present that can explain all the SSD variations within and between families. We hypothesize that differences in "predator strategies" between families of spiders present one viable way to study the proximate factors that are driving the evolution of SSD in the Araneae. It has been noted that a number of mechanisms may relate to foraging strategy (which is not a fitness component by itself but ultimately provides the energy for all life functions and thus affects most fitness components directly). Thus, we proposed that SSD within and between families of spiders may in part be due to differences in predaceous foraging strategies within and between spider families.

Abdominal traits were commonly used to estimate "body size" in previous studies. However, these may be better estimates of *body condition or current developmental state* (e.g., is the female well fed or starved, gravid or not gravid; are individuals immature or mature?). Because of this, several current researchers (Foellmer and Moya-Larano 2005) suggest using a *stable character* such as *carapace width* as the taxonomic character to establish size comparison between sexes (Foellmer and J Moya-Larano 2007: Chapter 7). This is because the vast majority of spiders exhibit determinate growth and do not molt after maturity (thus the carapace width is *static* at maturity). In addition, prosoma (cephalothorax) traits (especially carapace width) are highly correlated with body mass at maturation and therefore may provide the most accurate way of estimating a spider's size (Foelix 1996).

This study had two purposes; first, to conduct a biodiversity survey. This included the collection and identification of spiders within all habitats at PCCI as well as the creation of a synoptic collection that remains with the institute. The second component of the study was to attempt to determine if SSD in spider families is related to differences in their foraging strategies (e.g., is SSD more pronounced in web builder spiders compared to those with roaming or hunting strategies?) We expected to find greater degrees of SSD in families where males and females lived different lifestyles, specifically in regard to their predation strategies.

MATERIALS AND METHODS

Study Site

This 2014 summer-long study took place in southwestern Michigan at Pierce Cedar Creek Institute. PCCI, located in Hope and Baltimore Townships, Barry Co. Michigan, USA.

Spider Collection

Spiders were collected from the 661 acres of forest, prairies, wetlands, and aquatic habitats that make up the PCCI property. Samples were gathered using a variety of techniques (see below), and once captured, specimens were brought to the lab for observation, identification, measurement, and sometimes preservation.

Sweep netting was done weekly. Two large sweep nets (0.4 m diameter by 1.0 m length, rounded bottom) were constructed from white mosquito netting over bass net frames. To ensure that spiders with different diurnal and crepuscular activity would be captured, sweeping was done during the morning, afternoon, and at dusk. PCCI habitats included upland fields, open forest mesic prairie, and prairie fen areas.

Litter sampling was the primary collecting method in heavily wooded areas where thick layers of leaf debris were present. Litter samples were collected from the Little Grand Canyon area (primarily a mixed hardwood forest), as well as from the main property of PCCI. Leaf litter from field sites were stored in ziplock baggies and taken back to the lab. Once at the lab, the bags of debris were emptied into deep porcelain trays and sorted through. Spiders found in the leaf litter were transferred to mason jars and kept in the lab for identification.

Spider Rifle was used to capture spiders in tight, restricted spaces. This is a homemade device, constructed of inexpensive PVC tubing and operated by compressed air; a vacuum is created when the compressed air is released and the spider is sucked up through a tube into a holding chamber.

Miscellaneous Techniques:

Many spiders were found by simply hiking the trails of PCCI and visually locating spiders that were then captured by small plastic containers. Water-inhabiting spiders were captured in Cedar Creek, intermittent streams, and ponds of PCCI. Because many spiders are nocturnal animals, nighttime spider hunting was a successful way to locate a multitude of species. Areas surveyed at night were the young growth forests, and forested wetland areas, along with various points along the Cedar Creek.

I. Biodiversity Survey

According to PCCI's "November 2013 Species Inventory List," only six species of spider had been identified on the property since the institute's opening. The primary goal of the project was to establish a more comprehensive PCCI species list, and provide the institute with a synoptic collection. Spiders collected from PCCI were identified, and then organized by family and related families. Two-part identification labels were created with each specimen's scientific name and the location and date it was found.

Spider Preservation

Spiders have a hydrostatic skeleton.; when a spider dies its fluid pressure is lost and the body dries and shrivels.

For this reason, specimens were preserved in an 80% ethyl alcohol solution, 80% isopropyl alcohol solution, or frozen. Exposing specimens to freezing conditions for a few minutes, we used this method to sedate spiders for observation and measurement. Spiders that remain frozen retain color better than spiders kept in an alcohol solution. However, most specimens were placed in an alcohol solution, which made it possible to continue handling them easily for identification and measurement purposes.

Identification

Assistance for species identification was given by Dr. Allen Brady of Hope College, Dr. Cara Shillington of Eastern Michigan University, and Dr. Danielson-

Francois of the University of Michigan Dearborn. Useful keys and manuscripts, as well as techniques were also shared, and then repeated and used in the lab at PCCI.

Several spider identification books, and online keys were also used in the identification process: "Common Spiders of North America" (Bradley, 2012), "Spiders of the North Woods" (Webber, 2002), and "Spiders of North America: An Identification Manual" (Ubick and Cushing, 2009).

Spiders that were easily recognizable were identified and released, unless they were used as specimens for the synoptic collection. Many spiders were frozen or placed in an alcohol solution for later identification. Specimens were viewed under a dissecting scope and details such as hairs/spines, chelicerae length, eye arrangements, genitalia, etc. were observed to establish species identification. Spiders that could not be identified by the available resources were brought to the spider experts listed above.

II. SSD Measurement and Statistical Analysis

Specimens collected for biometric measurement were brought to the lab to first be properly identified. Specimen were kept in jars, or if juvenile, placed in terrarium environments to be given a chance to mature. These spiders were fed a diet of *Drosophila melanogaster,* as well as larger insects available from PCCI environments.

The most commonly encountered spiders on PCCI property were chosen as specimens to be measured for the SSD portion of the study. Within each species, we recorded sex (male/female) and then measure carapace width and length, in milimeters, using electronic calipers. From this data, averages were taken and the means of males and females *within* each species were compared using an unpaired t-test on GraphPad Software (La Jolla, CA).

RESULTS

I. Biodiversity Survey

The institute's species count went from 6 species to 40, a 700% increase in known species diversity. Forty species of spider were identified from thirteen spider families found at Pierce Cedar Creek Institute. A complete list of species is located in the Appendix.

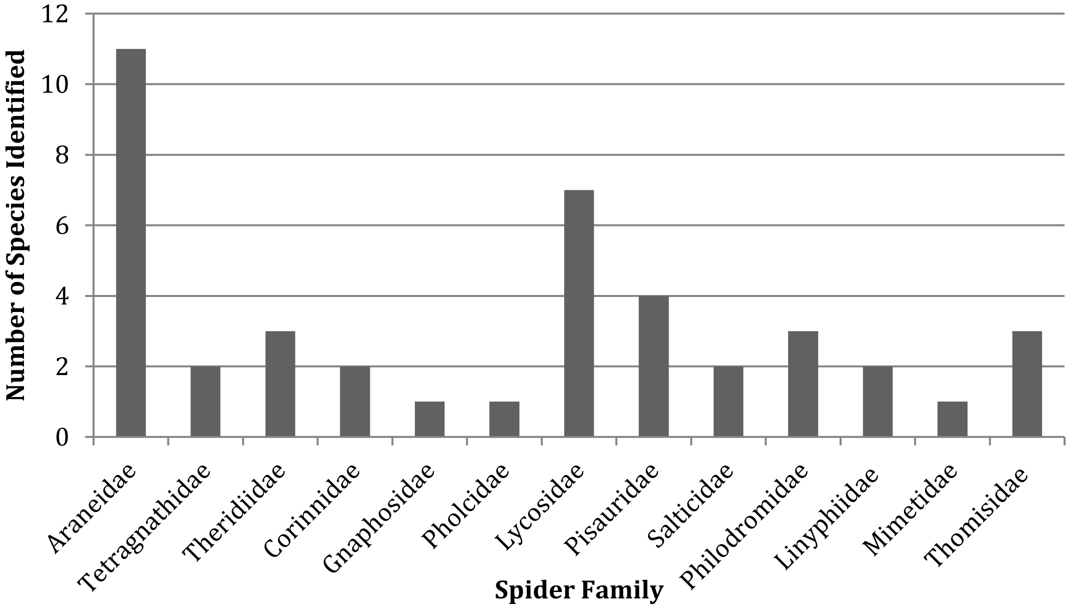

Figure 1. shows the number of species found in each family of Order Araneae at PCCI.

The two most common Order Araneae families at PCCI in relation to all other species were Araneidae and Lycosidae (Fig.2). Family Araneidae, the orbweavers, comprised about a quarter of the total spiders identified at PCCI over the summer of 2014. Eleven species of orbweavers were identified, with five species belonging to the genus *Araneus*. The species *Araneus* diadematus (cross orbweaver), was one of the most common spiders seen on the property. Other orbweavers of interest were: *Acanthepeira stellata* (starbellied orbweaver), *Mangora gibberosa* (lined orbweaver), *Argiope aurantia* (black and yellow garden spider), and *Micrathena gracilis* (spined micrathena).

Wolf spiders, Family Lycosidae , were the second largest group of spiders found at PCCI (Fig.2). A particularly important species to note was the wolf spider *Lycosa modesta*. This uncommon species was found near the Cedar Creek at the border of the sand prairie and adjacent woodline. Several immature individuals of *L. modesta* were identified from this area.

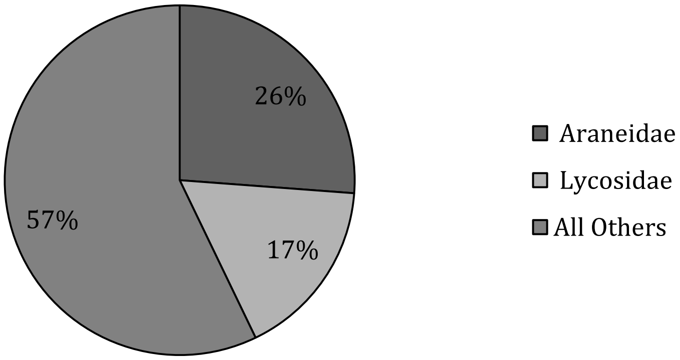

Figure 2. Proportion of Spider Families at PCCI.

Three members from Family Theridiidae were found, most notably *Latrodectus variolus,* the northern black widow. Both male and female widows were found at the sand prairie near the Cedar Creek. The most commonly encountered species of Family Theridiidae was *Theridion frondeum*, a small, brightly-colored cobweb weaver.

II. SSD Measurement and Statistical Analysis

Three species of web-building spider, and one species of non-web building spider were selected for measurement.

Table 1. Results from Unpaired t-Test

Species	P-value	t value	Standard Error of Difference
M. gibberosa	0.0017	3.4642	0.029
F. communis	0.4166	0.8414	0.126
T. eolngata	0.1394	1.55	0.114
P. audax	0.0282	3.0565	0.239

Table 2. Comparison of Species and Predatory Style by Sex

		Predatory Type		
Species	**Family**	**Female**	**Male**	**Size Comparison**
Mangora gibberosa	Araneidae	Web	Wandering	0.10 mm F > M
Frontinella communis	Linyphiidae	Web	Wandering	0.106 mm F < M
Tetragnatha eolngata	Tetragnathidae	Web	Web	0.176 mm F > M
Phidippus audax	Salticidae	Stalking	Stalking	0.731 mm F > M

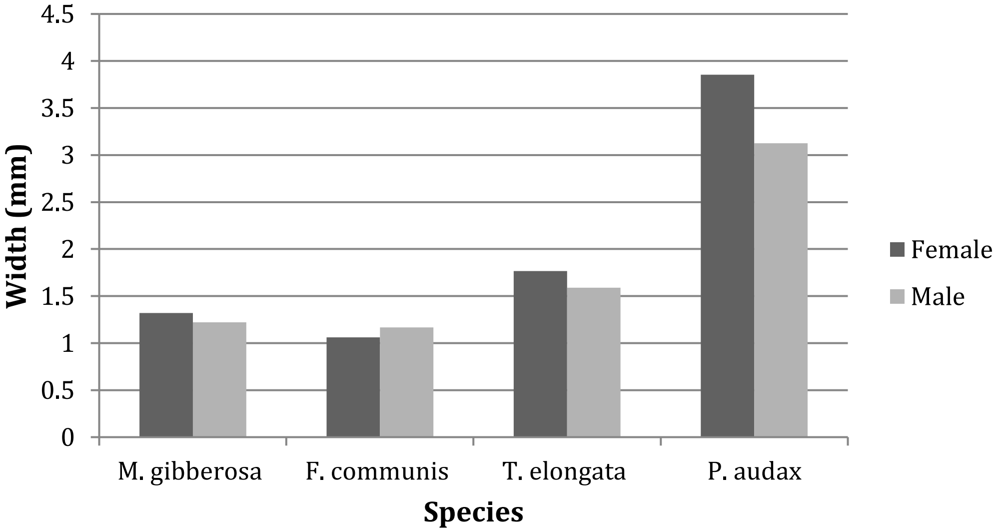

Figure 3. Average Carapce Width Measurements

Females had on average larger carapace measurements than their respecitve males in all species except *F. communis*, where males were generally larger (Fig. 3). The jumping spiders, *P. audax,* had the greatest size difference (0.731 mm) between the two sexes, and females were significantly larger than the males ($t_{df} = 3.06_{5}$, P = 0.028). Despite males and females of *M. gibberosa*, the lined orbweaver, having the smallest difference in carapace widths (0.10 mm), females were significantly larger than males in this species as well ($t_{df} = 3.46_{28}$, P = 0.002). There was no significant different in size between males and females of either F. communis $t_{df} = 0.84_{12}$ P = 0.417) or *T. elongata* ($t_{df} = 1.55_{16}$ P = 0.139).

M. gibberosa was considered to be the most significant becaue it had the largerst sample size. Females of this species built orb-shaped webs in fields, males were found in the same fields/prairies but wandering instead of on webs. Females “appeared” to always be slightly larger than males. The average carapace width for females was 1.32mm, whereas the average carapace width of males was 1.22mm. The probability value from the t-test was 0.0017 (Table 1), indicating the 0.10 mm difference in size between the sexes was very significant.

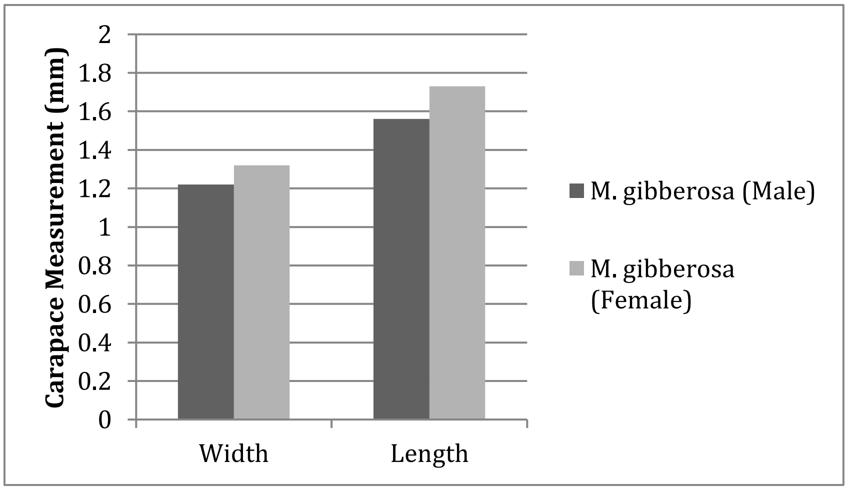

Figure 4. *M. gibberosa;* Comparison of Sexes Carapace Width and Length

The jumping spider *P. audax*, showed a significant difference in size between the sexes. As shown in Table 2, the average carapace width for females was 3.855mm, and males measured an average width of 3.124mm. The P-value for *P. audax* was 0.0282 (see Table 1), suggesting there was a statistically significant difference between male and female carapace means.

Two species showed no statistical difference using the unpaired t test results. *F. communis* was the only species where males had a larger average carapace width than females; the average carapace width of the male was 1.166mm, and the female's average was 1.06mm, a 0.106 mm difference. The long-jawed orbweaver had 0.176 mm difference in average size between the sexes; the male's average carapace width was 1.59mm, and the female's was 1.766mm.

DISCUSSION

I. Biodiversity Survey

A greater species diversity of Order Araneae than previously believed was discovered at PCCI. A total of forty species from thirteen families were identified between May 26th and August 26th 2014. New species were found continuously throughout the summer. The habitat diversity of the wooded areas, wetlands, prairies, and aquatic areas of PCCI likely accounts for the great diversity of spiders found.

Many PCCI species found were those that preferred humid or moist environments. Spider life relies heavily on humidity levels, temperature, light intensity, and prey abundance (Gillespie, 1987). Multiple wetland habitats comprise roughly 40%

of PCCI, with another 2% being open water in Brewster Lake, Cedar Creek and connecting streams, as well as in retention and vernal ponds. There were also high amounts of precipitation during the summer of 2014. According to National Climatic Data Center (NCDC), the total precipitation from June to August 2014 was 11.96 inches (304.78 mm), which is well above the normal average of 9.74 inches (247.40 mm). The high amount of precipitation may have enabled high growth rates in the flora and fauna of PCCI, which would have provided spiders with the greater abundance of potential prey we observed, and consequently increased spider population growth rates. Typical temperate habitats such as those at PCCI may support up to 800 spiders per square meter with a diversity of 20 species per hectare (Coddington and Colwell 2001).

II. SSD Measurement and Statistical Analysis

Four species of common spiders were chosen for SSD analysis because of their relative abundance and maturity upon capture. The orbweaver *Mangora gibberosa* (Family Araneidae) was collected from prairie habitats. From Family Linyphiidae (the sheet-weavers), *Frontinella communis*, was selected for measurement; the males and females of this species appear phenotypically different in color and abdomen shape. The third species chosen was a long-jawed orbweaver, *Tetragnatha elongata* (Family Tetragnathidae). These spiders showed an aggregative behavior in their web building, with males and females living in close proximity. The jumping spider, *Phidippus audax* (Family Salticidae), was selected as the fourth species to be measured; the females being noticably larger than the males. *P. audax* was the only non-web builing species measured.

We had hoped to include more than four species, but were unable to find sufficient numbers of mature specimens to represent the other famlies.

Neither male nor female jumping spiders build webs, yet males were noticeably smaller than females. Whereas *T. elongata*, both sexes inhabit webs, but there is no significant difference in size bewteen male and female. This could be due to the differences in predaceous strategies between the two species. Web building limits competition for food and space (Tahir, 2010); webs are able to decrease competition because of their inherent versatility in placement and prey capture. Both males and females of *T. elongata* were observed living on webs closely built together. Perhaps this lifestyle limits competition within the species and therefore a large degree of SSD does not occur.

The original hypothesis that SSD is related to differences in predation strategies was supported by some data, but not all of the data and therefore must be rejected. These data leans toward the idea that within the species of Order Araneae, SSD may have arisen by independent evolutionary pathways.

There are various factors, such as competition for resources or mate choice, that could influence the evolution of SSD within a species (Lande, 1980). An evolutionary origin of male dwarfism or female gigantism can only be understood with further analysis before its origin and maintenance can be explained in ecological and evolutionary terms.

It is extremely difficult to identify immature spiders with currently available taxonomic keys, and therefore not all of the spiders collected over the summer were identified. Many species do not reach full maturity until autumn, and our study had to reach a preliminary conclusion by the end of August. This was a major problem in regards to the SSD portion of the study. Spider families that we had intended to include were not mature by the time the study ended.

If this study were to be repeated, it would need to be done over a longer period of time to include spiders that mature later in the year, during late summer and early fall. Also, though carapace width is an okay measure we might include further measurements, such as abdomen length and width, and leg lengths, for greater comparison. While comparing males and females, it was noticed that abdomen size was much larger in web building females than in males of the same species.

CONCLUSION

The species diversity for the Order Araneae was found to be much greater than previously documented at PCCI. Spiders are an immensely diverse and abundant group; they are remarkable in their ability to inhabit almost all environments. PCCI offers diverse habitats, including several forest and prairie habitats, as well as multiple wetland and aquatic areas. The ecological diversity of PCCI land and favorable conditions throughout the summer account for the high biodiversity of spiders found at the institute.

We sought to test the link between predation strategy and SSD by looking at six families of spider and only one species per family. The four species studied were *Mangora gibberosa* (Family Araneidae), *Frontinella communis* (Family Linyphiidae), *Tetragnatha elongata* (Family Tetragnathidae), and *Phidippus audax* (Family Salticidae). Only *M. gibberosa* had a sample size large enough to show strong support for our hypothesis that the prevalence of SSD within spider families is partly due to the differences in predaceous strategies between and within spider families. Because not all of the data is supportive, our hypothesis is rejected as it stands. It is possible that SSD evolved independently throughout many different anagenetic lines of Aranaea. It may be that the examples of sexual size dimorphism in spiders can be best explained by distinctly different, and possibly unique explanations for each clade.

ACKNOWLEDGEMENTS

My faculty mentor Matthew Douglas for his assistance with this project.

Sara Syswerda, Biological Field Station and Education Director at PCCI, for her guidance and direction.

A collective thank you to the following arachnid experts for their time and assistance in identification and knowledge sharing:
Dr. Allen Brady of Hope College
Dr. Cara Shillington of Eastern Michigan University
And Dr. Anne Danielson-Francois of University of Michigan Dearborn

Pierce Cedar Creek Institute, The Willard and Jessie Pierce Foundation, and Undergraduate Research Grants for the Environment Program for the opportunity and resources to carry out this project.

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Appendix. List of Spider Families and Species in Order Araneae collected at PCCI from June through August of 2014.

Species Name	**Common Name**
Family Araneidae	Orbweavers
Araneus bicentenarius	Lichenmarked Orbweaver
Araneus diadematus	Cross Orbweaver
Araneus marmoreus	Marbled Orbweaver
Araneus cingulatus	
Araneus pratensis	
Mangora gibberosa	Lined Orbweaver
Acanthepeira stellata	Starbellied Orbweaver
Micrathena gracilis	Spined micrathena
Eustala anastera	
Hyposinga pygmaea	
Argiope aurantia	Black and Yellow Garden Spider
Family Tetragnathidae	Long-jawed Orbweavers
Leucauge venusta	Venusta Orchard Spider
Tetragnatha elongata	
Family Theridiidae	Cobweb weavers
Latrodectus variolus	Northern Black Widow
Theridion frondeum	
Theridula opulenta	
Family Corinnidae	
Meriola decepta	
Castianeira cingulata	Two-banded Ant Mimic
Family Gnaphosidae	
Herpyllus ecclesiasticus	Parson spider

Species Name	**Common Name**
Family Pholcidae	
Pholcus phalangioides	
Family Lycosidae	Wolf Spiders
Allocosa funera	
Rabidosa puntulata	
Pardosa moesta	
Tigrosa helluo	
Lycosa modesta	
Pirata piraticus	
Schizocosa sp.	
Family Liocranidae	
Agroeca pratensis	
Family Pisauridae	
Dolomedes triton	Fishing spider
Dolomedes scriptus	
Dolomedes tenebrosus	
Pisaurina mira	
Family Salticidae	
Tutelina elegans	
Phidippus audax	Bold Jumping spider
Family Philodromidae	
Philodromus cespitum	
Thanatus vulgaris	
Philodromus vulgaris	Running Crab spider
Family Linyphiidae	Sheetweavers
Frontinella communis	
Neriene radiata	
Family Mimetidae	Pirate Spiders
Mimetus sp	