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Does Pitcher Plant Morphology Affect Spider Residency?

Marc A. Milne[1,2] and Deborah A. Waller[2]

Abstract - Spiders are often found as residents in association with *Sarracenia purpurea* (Purple Pitcher Plant). Many spiders choose web locations based on environmental cues such as vegetation structure and composition, prey density, temperature, and humidity. To determine if spiders use cues from the Purple Pitcher Plant to build their webs, we conducted a field study using variants of the plant that separated various morphological features: nectar, pigment, and the presence of prey. There was no difference in spider residency across all treatments and no difference in male/female or mature/immature residency. Linyphiids were the most common residents, possibly due to pitcher structure and natural web size.

Introduction

Sarracenia purpurea L.(Purple Pitcher Plant) is a low-lying herbaceous perennial that uses pitcher-shaped leaves to capture mostly arthropod prey for nutrient supplementation. Common prey of the Purple Pitcher Plant include invertebrate taxa such as insects, spiders, harvestmen, mites, mollusks, and the occasional small vertebrate (Cresswell 1991, Heard 1998, Judd 1959, Lloyd 1942, Wray and Brimley 1943). Most carnivorous plants have been hypothesized to use morphological features such as nectar and red pigment to lure prey (Joel 1986, Juniper et al. 1989, Lloyd 1942, Schnell 2002). Other morphological features that may function in prey attraction or retention include ultraviolet (UV) reflectance (Joel et al. 1985), decaying insects in the liquid (Schnell 2002), and fragrance (Di Giusto et al. 2008, Juniper et al. 1989), yet many of these features have not been well studied. However, some studies have shown that red pigment has little effect on prey capture, because naturally occurring pitcher plants that lack the gene to produce red pigment (such as *S. purpurea* ssp. *purpurea* f. *heterophylla* (Eaton) Fernald) have similar capture rates to pigmented varieties (Green and Horner 2007, Sheridan et al. 2000). Moreover, some studies have concluded that carnivorous plants may rely heavily on random encounters to catch prey and that these morphological features merely retain prey on the plant (Williams 1976, Zamora 1995).

Spiders can be separated into two main groupings by their method of prey capture: web-building spiders and ground spiders (Foelix 2010). When selecting habitats, many types of spiders choose areas based on prey density (Harwood et al. 2001, Kareiva et al. 1989, Riechert 1985, Waldorf 1976), vegetation structure (Duffey 1966, Halley et al. 1996, Post and Riechert 1977, Riechert 1974, Robinson 1981), vegetation composition (Barnes 1953, Post and Riechert 1977), and abiotic factors such as temperature and humidity (Enders 1977, Riechert 1985,

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Tanaka 1991, Turnbull 1964). The distribution of spiders is also affected by seasonal changes; population peaks of spiders usually occur in the late spring and early fall (Barnes 1953, Elliot 1930, Muma and Muma 1949).

Spiders frequently build webs near carnivorous plants and sometimes steal prey from them (Schnell 2002). Alternatively, one study has shown that spiders avoid areas of high carnivorous plant (*Drosera capillaris* Poiret [Pink Sundew]) density to avoid competition (Jennings et al. 2010). However, when living near the Purple Pitcher Plant, certain spiders of the family Linyphiidae have been shown to be kleptoparasitic because they spin webs inside of the pitcher and consume prey that would have otherwise gone to the plant (Cresswell 1991, 1993). Spiders of the family Lycosidae have been hypothesized to have a commensal role by using decaying or dead pitchers as oviposition sites (Hubbard 1896, Jones 1935, Milne 2012, Rymal and Folkerts 1982). Finally, the Purple Pitcher Plant may create a high insect density near the plant, making the immediate vicinity an appealing spot for spiders' webs. If spiders seek out pitcher plants, they may use certain morphological features (e.g., red pigment, nectar, dead insects, structure, etc.) to find them.

In a field study, we used five manipulated variants and/or models of pitcher plants that combined one or more of the following cues: red pigment, nectar, and/or decomposing prey. We then collected spiders residing near these treatments over three summer months to determine if the morphological features commonly found on carnivorous plants influence the behavior of spiders to reside nearby.

Field-Site Description

The field site was Old Dominion University's 129-ha (319-acre) Blackwater Ecological Preserve (BEP; 36.87°N, 76.83°W) in southeastern Virginia. BEP is a fire-dependent community dominated by *Quercus laevis* Walter (Turkey Oak) and *Pinus taeda* L. (Loblolly Pine), with many herbaceous shrubs and open spaces with low-lying plants (Frost and Musselman 1987). *Pinus palustris* Mill. (Longleaf Pine) is being restored at BEP, which is subjected to prescribed burns at least once a year. The preserve contained approximately 17 Purple Pitcher Plant clumps at the time of sampling, between May–July 2008.

Methods

Five different treatments were used in this study: the Purple Pitcher Plant with no manipulation (containing nectar [N+], red pigment [P+], and water [W+] in the pitchers; henceforth "N+P+W+"), *S. purpurea* ssp. *purpurea* f. *heterophylla* with no manipulation (lacking red pigment [P-]; henceforth "N+P-W+"), the Purple Pitcher Plant with nectar glands covered along the lip (peristome) of the pitchers (lacking most of the nectar [N-]; henceforth "N-P+W+"), the Purple Pitcher Plant with cotton placed into the pitchers to prevent prey capture (lacking water; henceforth "N+P+W-"), and blue polyurethane Purple Pitcher Plant models (lacking both nectar [N-] and red pigment [P-]; henceforth "N-P-W+")

(Fig. 1). Although this experimental setup presents some minor limitations (e.g., cotton-filled pitchers do not allow for spiders to reside within the pitchers, models are not green like other treatments), the main morphological features are effectively separated using this design. Five replicates of each of these treatments (25 total) were created. Plants and models were modified so that each had five pitchers. For live treatments, flower stalks were cut off early in development to prevent flowering.

Each N-P+W+ had its peristome covered with a clear, quick-hardening sealant (Lexel super-elastic sealant, Sashco Sealants, Inc.). In a preliminary study, slices ≈1 mm thick were cut from the peristome of sealed pitchers and mounted on a slide. Examination of slides under light microscopy at 20x revealed that this sealant covered the stomata on the epidermal surface and therefore plugged any other glands associated with nectar production.

To minimize the effect of variable prey availability, treatments were randomly placed within a 100-m x 100-m area. This area was adjacent to naturally growing pitcher plants and vegetation similar to areas at BEP where natural populations of Purple Pitcher Plant grew. All plants were kept in pots (16.5 cm diameter x 18.4 cm depth) and placed into the soil so that the top of each pot was flush with the ground. Leaf litter from adjacent areas was spread at the base of the plants and the plant models so that it resembled the surrounding area. Manipulations of the plants to create the different treatments were conducted on the first day of setup. All treatments were watered every day of data collection. The area of pitcher openings was measured and recorded twice during the study for all treatments except N+P+W- because the opening was filled with cotton and therefore a spider could not reside within it.

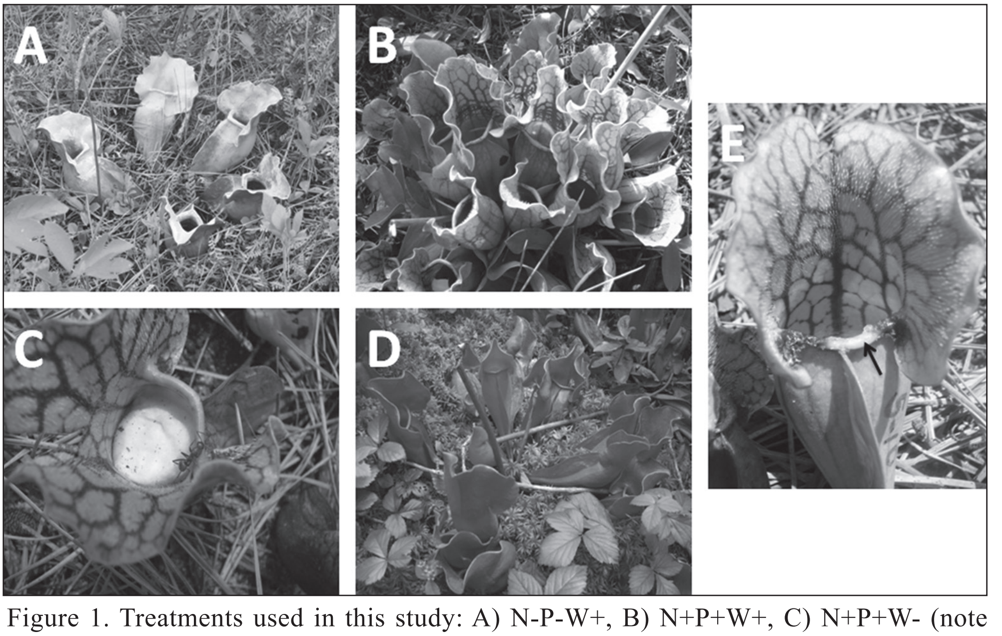

Figure 1. Treatments used in this study: A) N-P-W+, B) N+P+W+, C) N+P+W- (note cotton in pitcher), D) N+P-W+, and E) N-P+W+ (arrow indicates coated peristome).

Treatments were allowed to equilibrate in the surrounding area for one week prior to data collection. After this time period, all spiders found walking on, inhabiting a web directly over (<≈5 cm), inhabiting a web attached to, or inhabiting a web inside the pitchers of all plants and models (henceforth termed "residents") were removed three times a week for four weeks and then once a week for a month. The position (web over pitcher, web inside pitcher, or web against pitcher) of residents was recorded, after which they were collected and preserved for later identification. Residents were identified to species using Ubick et al. (2005) and other taxonomic keys.

Differences in the total number of female and male, immature and mature, or ground and web-building residents were each separately analyzed via a Wilcoxon rank-sum test using SPSS (IBM SPSS Inc., SPSS Statistics v. 20, Chicago, IL). Differences among treatments in the number of ground, web-building, and total residents were each separately analyzed via a Kruskal Wallis test in SPSS, as was the difference in the size of pitchers among treatments. SPSS was also used to run Fisher's exact tests to determine significant differences between the number of adult and immature residents in Linyphiinae and Erigoninae. Permutation chi-square tests were conducted using SAS (SAS Institute, Inc., SAS v. 9.3, Cary, NC) to determine the difference between adult and immature residents in the placement of their webs for the erigonines, linyphiines, and total linyphiids.

Results

Eight families of spiders were found among 123 collected residents (Table 1). Web-building residents were found significantly more often than ground-spider residents (Wilcoxon test = 465.0, z = -3.41, $P < 0.001$; Fig. 2). However, there was no significant difference among treatments in the number of ground (Kruskal Wallis test: $\chi^2 = 1.82$, df = 4, $P = 0.77$) or web-building residents (Kruskal Wallis test: $\chi^2 = 1.77$, df = 4, $P = 0.78$; Fig. 2). There was also no significant difference among treatments in the total number of residents found (Kruskal Wallis test: $\chi^2 = 2.09$, df = 4, $P = 0.72$; Fig. 2).

Table 1. Total number of spider residents found for each family across all treatments

Taxon	Number of residents found
Agelenidae	1
Araneidae	1
Dictynidae	1
Erigoninae (Linyphiidae)	27
Linyphiinae (Linyphiidae)	61
Lycosidae	8
Salticidae	11
Tetragnathidae	1
Theridiidae	3
Unknown immatures	9

Approximately half of all of the spiders in webs were adults (49.5%), and the other half were immature (50.5%). There was no significant difference among all treatments between the number of female and male (Wilcoxon test = 590.0, z = -0.95, P = 0.34; Fig. 3a) and between the number of mature and immature (Wilcoxon test = 635.0, z = -0.05, P = 0.96; Fig. 3b) residents found.

The mean area of pitcher openings was 5.28 cm^2 (n = 200; SE = 0.21). The first measurement, taken during the early part of the study (mean = 5.14; n = 100; SE = 0.29), only slightly differed from the second measurement, taken later (mean = 5.41; n = 100; SE = 0.30). N-P-W+ had a significantly greater pitcher size than the other treatments (Kruskal Wallis test: χ^2 = 58.8, df = 3, P < 0.001): N+P-W+ (mean = 4.05; n = 50; SE = 0.23); N-P+W+ (mean = 3.48; n = 50; SE = 0.30); N+P+W+ (mean = 3.94; n = 50; SE = 0.24); N-P-W+ (mean = 9.62; n = 50; SE = 0).

The most common residents were spiders in the sheet-web weaving family, Linyphiidae. Due to the abundance of this family in our study, we concentrated much of our analysis on their numbers. The most common linyphiids found were: *Agyneta* morphospecies 1 (16), *Ceratinopsis interpres* Emerton (12), and *Agyneta* morphospecies 2 (7) (*Agyneta* is a difficult genus to identify to species, so specimens were separated into morphospecies). Linyphiids accounted for 83.5% of the spiders in webs near the plant. Most linyphiid webs were built against the pitcher as opposed to over or within the pitcher (Permutation test: χ^2 = 11.46, df = 2, P = 0.003; Fig. 4).

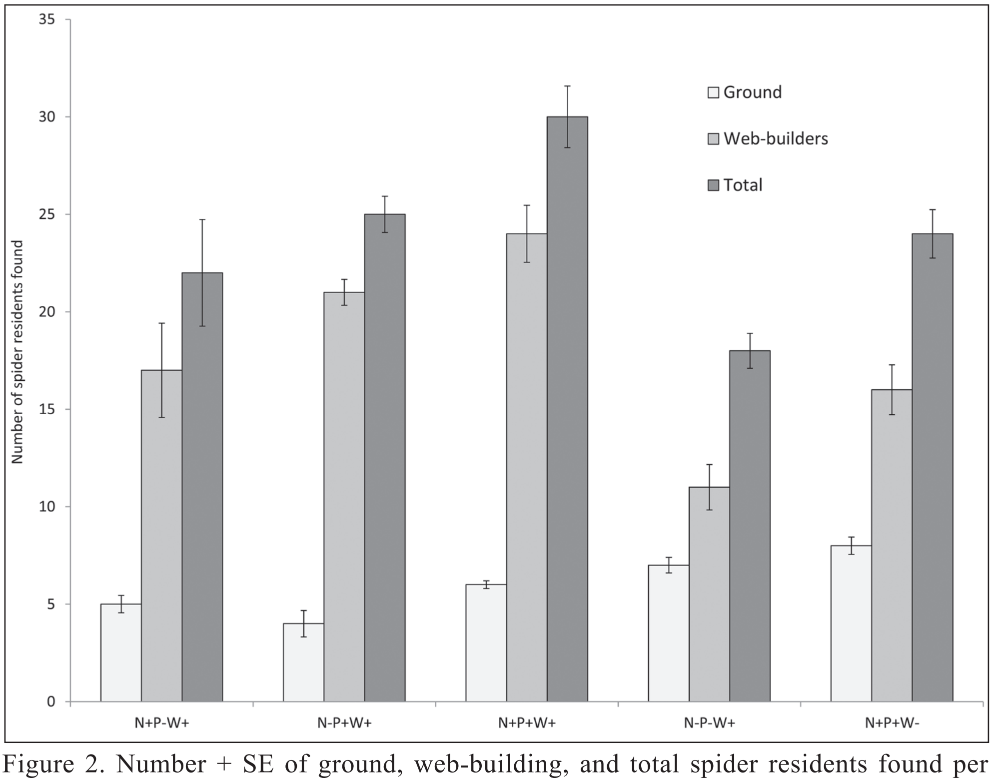

Figure 2. Number + SE of ground, web-building, and total spider residents found per treatment type.

Members of the linyphiid subfamily Linyphiinae were three times more abundant as residents compared to members of the linyphiid subfamily Erigoninae. A greater number of linyphiine residents were adults rather than immature (Fisher's

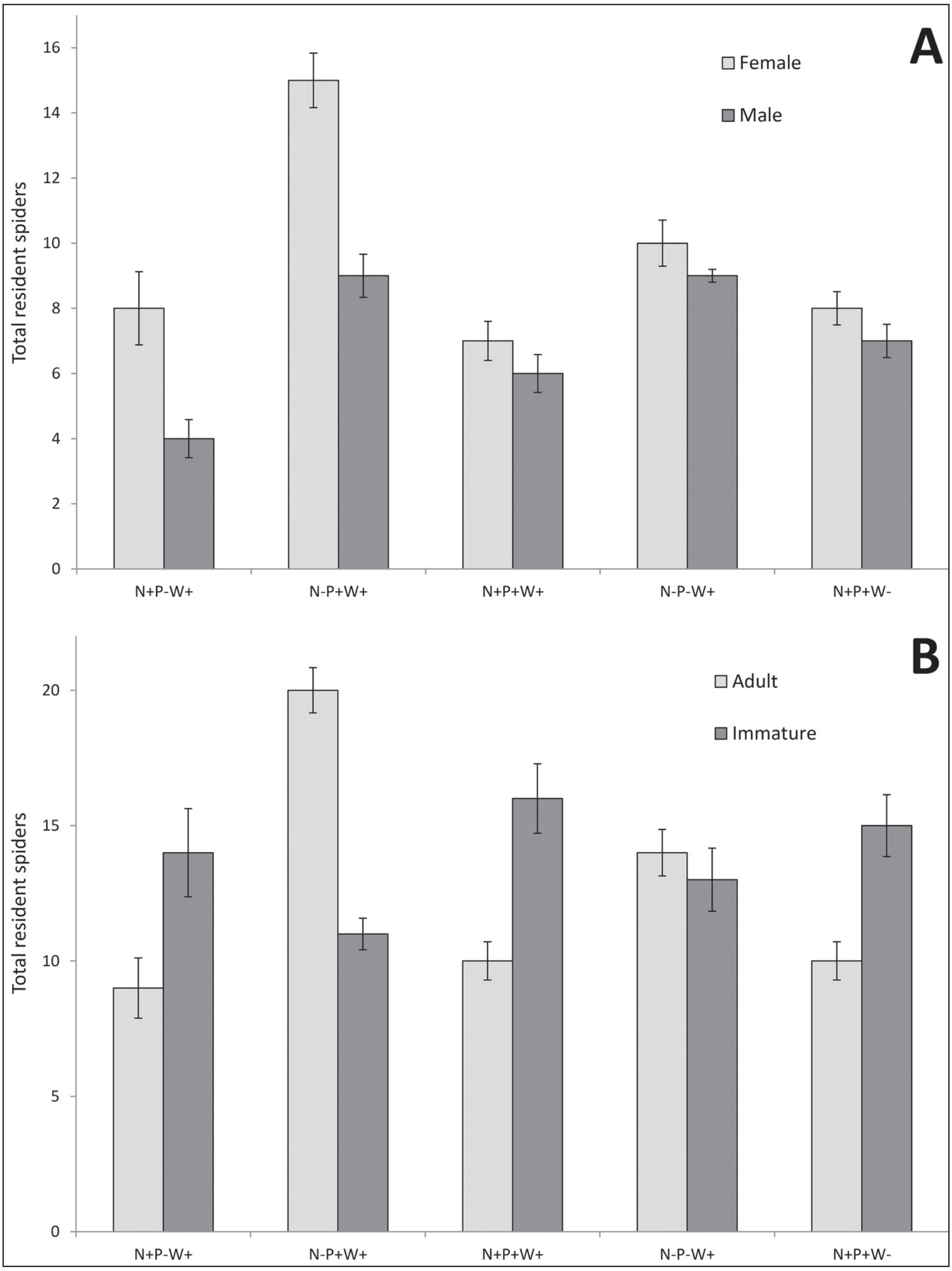

Figure 3. (A) Total number of female and male resident spiders near pitchers per treatment type; (B) Total number of mature and immature resident spiders near pitchers per treatment type.

exact test: $P < 0.01$; Fig. 4). However, there was no significant difference between the residency rate of adult versus immature erigonines (Fisher's exact test: $P = 0.82$; Fig. 4). Linyphiines were more likely to build webs against the pitcher than inside or over the pitchers (Permutation test: $\chi^2 = 14.45$, df = 2, $P < 0.001$), although this trend was non-significant in the erigonines (Permutation test: $\chi^2 = 0.636$, df = 2, $P = 0.82$; Fig. 4). All other residency comparisons between maturity and web location were non-significant.

Discussion

This is the first study in which the morphological features of a carnivorous plant were isolated in an attempt to determine their individual effects on spider residency. Three conclusions may be inferred from these data: 1) the morphological features of the Purple Pitcher Plant do not influence how often spiders resided on or over the plant, 2) there was no significant differences in the sex or maturity level among the spider residents over all treatments, and 3) spider residents often build webs inside pitchers when regular web size is similar to pitcher opening size.

The lack of difference among treatments in the density of residents found suggests that spiders were non-selective for the presence of the tested Purple Pitcher Plant features when choosing a living site. Spiders encountering the Purple Pitcher Plant fell victim to the plants or built webs near them. They did not appear to

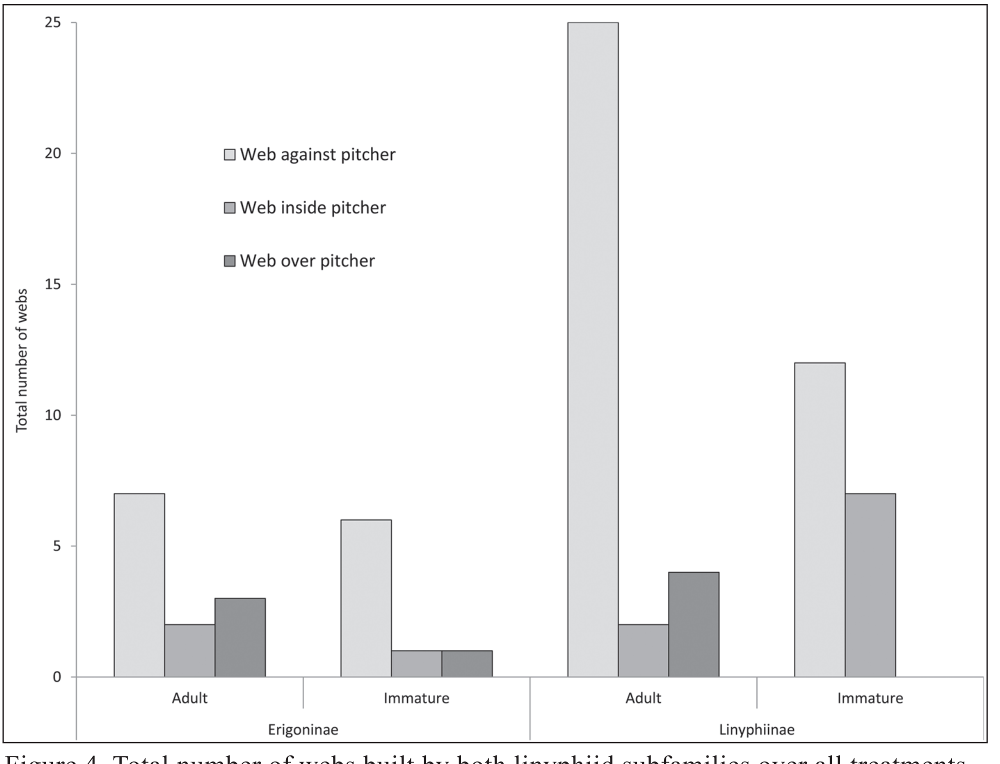

Figure 4. Total number of webs built by both linyphiid subfamilies over all treatments.

seek out plants with high amounts of dead prey (Cresswell 1991, 1993) because there was no preference for treatments that held dead prey versus the cotton-filled pitchers that lacked prey. However, the lack of a significant difference among our treatments in the rate of spider residency may have been a result of our low sample size (only five replicates of each treatment type). Moreover, further studies may be warranted to test if spider prey density near the Purple Pitcher Plant is higher than spider prey density further from the plant, as a significant difference may have also influenced the results.

Female spiders lead a largely sedentary lifestyle and are likely to be found in webs, while adult males often wander, looking for females, and immature males are largely confined to their webs or retreats (Foelix 2010). Therefore, adult males are more likely to be resident wanderers, crawling on the plant, while females and immature males are more likely to be sedentary residents. Although there was no statistical difference between male and female residents, there was a trend for females to be residents more often (Fig. 3). A sampling bias may have affected these values; our sampling method may have been biased towards web-builders because transient ground spiders were less likely to be found within the short time the plants were checked.

The most common residents, linyphiids, are sheet-web weavers that build sticky horizontal webs (Foelix 2010) based on the presence of vertical structures for support (Halaj et al. 2000, Samu et al. 1996), which were most often against Purple Pitcher Plant pitchers (Fig. 4). Linyphiids normally build webs at about 10 cm off the ground (Sunderland et al. 1986a), a height similar to that of Purple Pitcher Plant pitchers. Therefore, it is possible that this association is coincidental. More studies must be conducted to determine if more spiders reside near the Purple Pitcher Plant as opposed to away from the plant.

Linyphiids may be divided into two main subfamilies: Erigoninae and Linyphiinae. As adults, erigonine spiders commonly build webs about 3–8 cm^2 in area (Harwood et al. 2001, Sunderland et al. 1986b), a size range that corresponds to the mean area inside the pitchers in our treatments (5.28 cm^2). Therefore, the insides of pitchers might seem like ideal web locations for adult erigonines, but the slipperiness of the inner walls may have led to high death rates of these spiders, lowering the number of adult erigonines found in webs inside pitchers in this study. This hypothesis is supported by the high number of dead erigonines found captured in the pitchers during this study (M.A. Milne, pers. observ.).

Similarly, linyphiines often choose web sites based on the presence of vertical structures to support their webs (Halaj et al. 2000, Samu et al. 1996). Adult linyphiines build webs from 16 cm^2 (Sunderland et al. 1986b) to 74cm^2 (Harwood et al. 2001) in area and immatures build a smaller web (<16 cm^2; Harwood et al. 2001). These mean web sizes, when compared to the mean area of the pitchers used in this study, may explain why more immature linyphiines were found in webs inside pitchers than adults (Fig. 4). Therefore, although there was a lack of selection for residency near specific treatments due to differences in which morphological features were present, there may have been a selection by erigonines and immature linyphiines for the interior pitcher size presented by the Purple Pitcher Plant and models.

This study provides evidence for the hypothesis that spiders do not reside near the Purple Pitcher Plant due to any unique morphological feature possessed by the plant. Although it was hypothesized that the prey captured by the Purple Pitcher Plant would attract spider scavengers, spider density was just as high near plants that did not have captured prey. It is therefore possible that spiders treat carnivorous plants as any other type of vegetation of that height. Moreover, further experiments should test the hypothesis that spiders view the Purple Pitcher Plant as competition and therefore avoid the plant, as has been seen with another carnivorous plant, the Pink Sundew (Jennings et al. 2010).

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