Resource Partitioning in *Sarracenia purpurea* Based on Pitcher Color

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Abstract

Resource partitioning is found in situations where two or more species have divided the use of essential resources in order to avoid competition. In some environments, such as bogs, where nitrogen is extremely limiting, plants like *Sarracenia purpurea*, the purple pitcher plant, have evolved modified leaves that acquire nitrogen through the capture and digestions of insects. Unlike most plants, whose leaves look identical and have the single function of carbon capture, pitchers have the dual function of both carbon and nitrogen capture and vary remarkably in green and red color. It is possible that pitchers on an individual plant exhibit color polymorphism as a mechanism to partition prey resources and maximize prey capture. We hypothesized that pitchers that were more similar in color would capture more similar types of prey than pitchers of more different color on the same plant. We sampled and analyzed prey of three pitchers (two of similar and one of different color) from 25 *S. purpurea* plants at Mud Lake Bog in Cheboygan, MI. We found that there is no evidence of a relationship between color difference in pitchers on the same plant and differences in types of prey captured. Our results did show however, that pitchers of bigger hoods tend to capture flying insects while smaller hoods favor capture of crawling insects, inferring that there may be a mechanism of resource partitioning through variation of hood sizes.

Introduction

Resource partitioning, the differential use of limiting nutrients or resources by different species, is an evolved response selected to reduce past competition and allow species with similar resource requirements to coexist (Schoener 1974). There are several examples of resource partitioning in nature where sympatric species differ in one of more traits such that they use a shared resource in different ways. For example, Lambert (1989) found that different fig-eating bird species in Malaysia partition figs based on size. Larger bird species ate larger figs while smaller bird species ate smaller figs. Another study suggests that bumblebees in Maine partition flowers species based on bee tongue length (Heinrich 1976).

In nature, the vast majority of plants have leaves that serve one primary function: capturing carbon. As a result, leaves on the same plant are essentially identical in appearance. In some environments however, such as bogs, nitrogen is extremely limiting. In bogs, *Sphagnum* moss forms in thick mats and creates an acidic environment that limits decomposition and, therefore, nitrogen availability. *Sphagnum* does this by releasing hydrogen ions in exchange for cations such as calcium and potassium (Soudzilovskaia *et al.* 2010). In response to low nitrogen availability some bog plants have evolved modified leaves that capture and digest insects (Vitousek *et al.* 1997). Unlike the leaves of most plants, the leaves of these carnivorous plants serve two functions: to capture carbon and to capture nitrogen by trapping insects (Fong and Bradley 2010).

Sarracenia purpurea, the purple pitcher plant, has pitcher shaped leaves that capture both insects and rainwater. Insects are attracted by the hood of the pitcher as well as the nectar inside the leaf. Hairs on the pitcher hood reduce insects' ability to walk, and they often fall into the pitcher. Once inside, it is difficult to crawl out due to the waxy surface on the inside of the pitcher, so the insects drown in the water (Nastase and Newell 1998). Because *S. purpurea* does not secrete digestive enzymes, each pitcher houses decomposers, or inquilines, that break down insect prey and release soluble nitrogen that the plant can use for development (Ellison and Gotelli 2002). Inquilines are typically bacteria, mosquito and midge larvae, and mites (Nastase and Newell 1998).

Unlike most plants, pitcher plants have polymorphic pitchers that vary in red and green coloration. Like other carnivorous plants, *S. purpurea* pitchers capture both nitrogen and carbon. Green coloration allows capture of carbon by photosynthesis and red coloration facilitates nitrogen capture by attracting insects (Joel and Gepstein 1985). It is possible that variation in color between individual pitchers on the same plant could be a mechanism of resource partitioning. For instance, green leaves may capture some types of prey while red leaves capture other types of prey.

A number of studies suggest that color traits are associated with higher capture rates. For instance plants with more red coloration and venation may capture more insects (Nastase and Newell 1998). Similarly, Shaefer and Ruxton (2007) found that insects are more attracted to red pitchers than green pitchers. These studies correlate red coloration with more prey capture overall rather than specific prey types. If one color is most advantageous for trapping insects, why then aren't all pitchers on an individual plant the color that maximizes prey capture? Why do pitchers on the same plant differ in color?

One possible explanation that has received far less attention is that natural selection favors having different colored leaves because polymorphism maximizes prey capture. Plants with both redder and greener pitchers might capture more types of insects overall than plants with all similarly colored pitchers. It is possible that color polymorphism helps eliminate intra-individual competition through resource partitioning; pitchers on the same plant may differ in color to capture a wider variety of prey types.

The same logic could apply to other characteristics that differ between pitchers on an individual plant. For example, this reasoning could be extended to aperture size. A past study found that pitchers with larger aperture size catch more prey than smaller pitchers (Cresswell 1998). It is also possible that on a plant, pitchers have different aperture sizes to capture different sized prey. Similarly, this reasoning could be applied to hair density on pitcher hoods. It is possible that plants may vary in hair density to affect capture and escape of different insect types.

Accordingly, in this study we ask if different colored pitchers on the same plant attract different types of prey. More specifically, we predict that pitchers on the same plant that are more similar in color will attract more similar prey types than pitchers on the same plant that are different in color. If so, we then ask if the difference in prey types reflects the magnitude of difference in color between two pitchers on the same plant. Following similar logic we ask if prey type captured differs between pitchers with different size, aperture size, hood size, and hair density on the same plant.

Materials and Methods

Study System:

In this study, we examined 25 *S. purpurea* plants in Mud Lake Bog in Cheboygan County, Michigan. At this site, *Sphagnum* moss creates very acidic conditions with an average pH of 3.25 (Small 1972). Ninety percent of our samples were taken from the east side of the lake to better standardize light and wind conditions that could possibly affect insect capture. Ten percent of our sample was taken from other parts of the bog to determine if prey types were different at other sites (Figure 1).

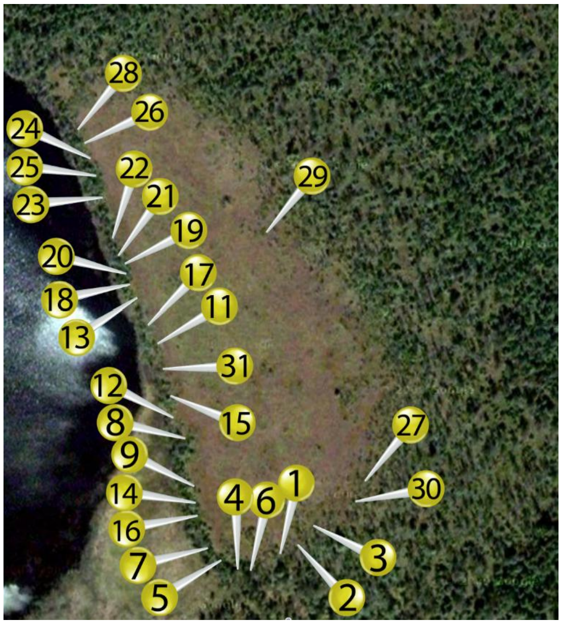

Figure 1: Aerial view of Mud Lake Bog, displaying sample locations.

Data Collection:

Sample Collection:

Within each plant three individual pitchers were sampled, two similar in color and one different in color. Two greener pitchers and one redder pitcher were sampled on 14 plants and two redder pitchers and one greener pitcher were sampled on 11 plants. The contents of each pitcher were collected first by using a turkey baster to suction water and most of the organisms inside, and second by injecting a syringe (10cc) filled with de-ionized water into the base of the pitcher to make sure no small particles were left behind the pitcher. Each pitcher was photographed. When selecting plants, those that had pitchers relatively equal in size were chosen in order to minimize the effect of pitcher size on prey capturing efficiency. We assumed that prey had access to all of the pitchers on an individual plant. We eliminated pitchers covered in spider webs from our sample because Hart *et al.* (2009) suggests that spider webs overlaying pitchers decreases capture by 10%. In order to determine whether other characteristics could affect prey type in pitchers, we also measured the length of the pitcher from the ground to the top of the hood, the width of the pitcher, the length and width of the aperture, and the height and width of the hood.

Color Determination:

In order to quantify the degree of similarity in color between pitchers, the photographs taken during the initial sampling were analyzed using Photoshop to determine the percentage of red on each pitcher hood. Using the magic wand tool/quick selection tool we selected the entire hood of the pitcher. The total number of pixels in the selection was noted via the histogram window. In order to analyze the pixels of green and red on the hood we used the select → color range tool. Using the eyedropper tool, we selected a red value as close to the red mean value as possible (which is also displayed in the histogram window). This second selection constituted the red portion of the plant (Figure 2). The number of red pixels was divided by the total hood pixels to give the percentage of red on each hood.

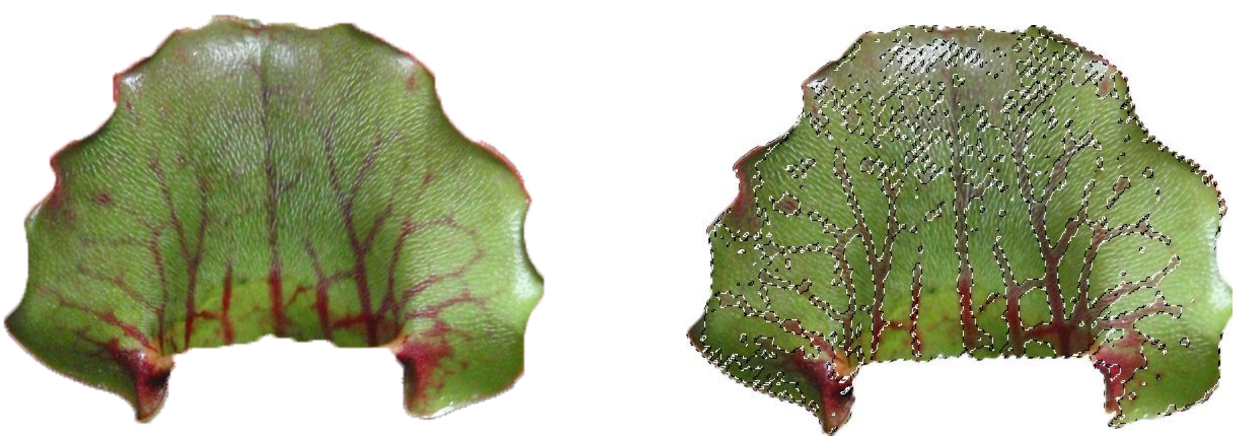

Figure 2: A) The pitcher hood on the left is an example of total area measured for color. It is the combined area of green and red. **B)** The pitcher hood on the right shows the area selected to measure the amount of red pixels using Photoshop. The area within the dotted lines is the area used to quantify the number of red pixels and used to determine the percentage of red on the pitcher.

Insect Identification:

The contents of each plant were inspected under a dissecting microscope. Organisms were identified as specifically as possible. We chose to limit sampling to fully or mostly intact insects and head capsules because only these parts of prey bodies were sufficiently complete for identification. Each time a new species was identified it was placed in a vial containing 70% EtOH and used as a reference for later comparisons.

Statistical Analysis:

For each plant we performed three paired t-tests (N=25 for each) using SPSS in order to determine whether the difference in prey types between similar and different pitchers was significant. We first determined what prey types were present in each pitcher. We then found the total number of prey types that were different between pitchers of similar color, and also between the two pairs pitchers of different color on the same plant. We labeled the two similar colored pitchers 1 and 2 and the different colored pitcher was pitcher 3. We named the total number of prey types that are different between pitchers of similar color 1 vs. 2 (Similar). The total number of prey types different between pitchers of different color was labeled 1 vs. 3 (Diff1). The number of prey types different between the second pair of different colored pitchers was called 2 vs. 3 (Diff2).

Because Photoshop was able to quantify color in more detail than the human eye can, we performed a linear regression of the number of different prey types vs. difference in percent red between each pair of pitchers on the same plant (N=75).

In order to determine the effect of color variation on prey types captured, independent of the effects length of the pitcher from the ground to the top of the hood, the width of the pitcher, length and width of the aperture, and height and width of the hood, we performed an ordered multiple regression in which all variables other than color were entered at step one and percent red was entered at step two. Because we also measured hair density, for only 5 samples rather than 25, we separately regressed differences among pitchers in prey type differences against hair density.

Results

Insect Identification:

Of the 303 individuals identified in the 75 pitchers sampled, 78 different insect species were classified. The most common orders found were Diptera, Hymenoptera, Acari, Coleoptera, and Araneae. The most common prey types identified were mites, Phoridid flies (scuttle flies), Calyptrate muscoid flies, Chironomid midges, Culicid mosquitos, Myrmecinae ants, and wasps. Least common prey types captured included crickets, salamanders, dragonflies, Membracid planthoppers, and moth flies (Psychodidae).

Do pitchers of more similar color on the same plant attract more similar types of prey than different colored pitchers on the same plant?

The average number of different types of prey caught between pitchers1 vs. 2 was 5.6. On average, 1 vs. 3 caught 5.92 different types of prey. The number of different prey types captured by 1 vs. 2 was not significantly different than the average number of different prey types captured by 1 vs. 3 (paired t-test= -0.539, d.f.= 24, p=0.6 : Figure 3). Pitcher pair 2 vs. 3 on average captured 6.48 different prey types, which was nearly significantly different from the average number of different prey types captured by 1 vs. 2 (paired t-test= -1.756, d.f.= 24, p=0.09: Figure 3).

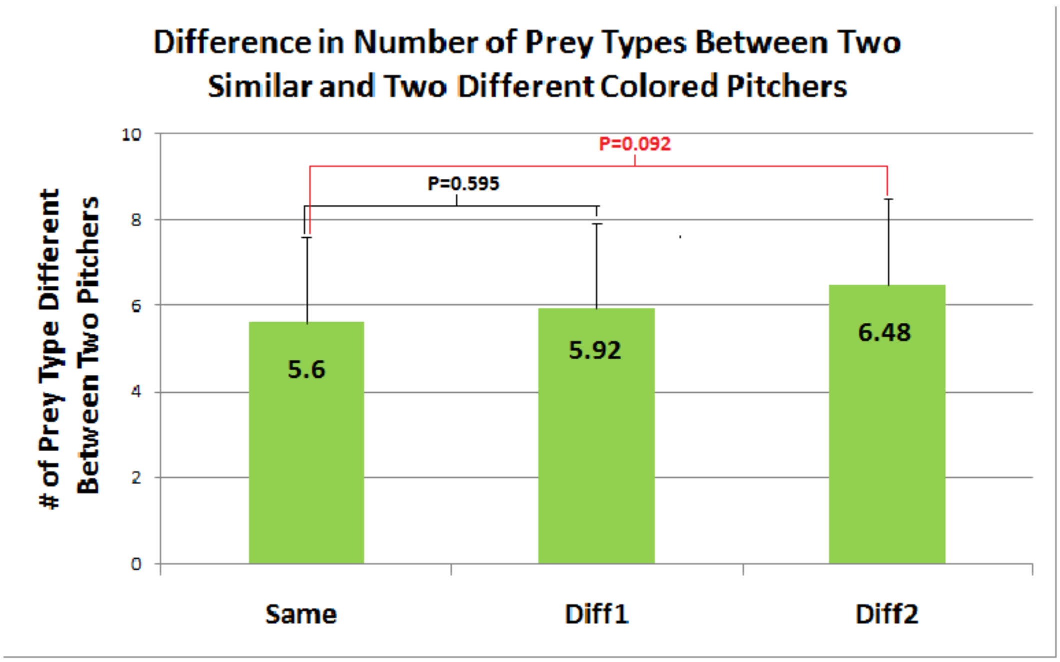

Figure 3: Compares the average number of different prey types caught between 1vs2 (Similar colored pitchers on the same plant), 1vs3 (Different colors pitchers on the same plant), and 2vs3 (different colored pitchers on the same plant) across all plants.

Does difference in redness influence difference in prey types captured?

There does not appear to be a relationship between variation in redness and variation in prey types captured across all pitchers (N=75). There is a weak negative correlation between magnitude of redness and magnitude of variation in prey types captured. Difference in prey types captured does not significantly differ with varying redness for the pitchers sampled (R^2=0.013, d.f.= 74, p>0.3: Figure 4).

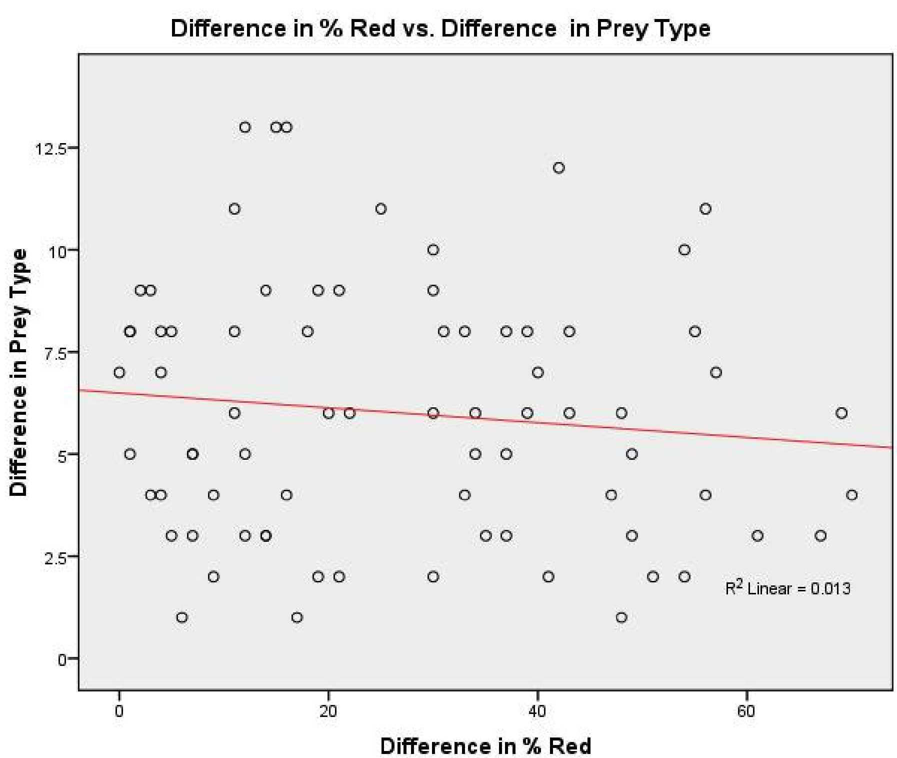

Figure 4: Figure 4 shows a weak negative correlation between redness and difference in prey types captured. Each point represents a pair of pitchers on the same plant.

Could other factors obscure a relationship between difference in redness and difference in prey types?

After statistically factoring out size variants that could be masking the effect of percent redness on prey capture, there was not a significant correlation between redness and difference in prey types captured (R^2=0.127, d.f. = 74, p=0.8: Table 1). Despite statistically eliminating the possible effect of overall size, aperture size, and hood size on prey capture, there was not a significant relationship between redness and variation in captured prey types.

Table 1: Step one shows an ordered multiple regression to standardize size variants before comparing difference in prey type with percent redness. Step two displays a multiple regression with standardized size values. Note that hood width shows a significant relationship with differences in prey type captured.

`Coefficients[a]

Model		Unstandardized Coefficients		Standardized Coefficients	t	Sig.
		B	Std. Error	Beta		
1	(Constant)	4.539	.972		4.668	.000
	LengthDiff	-.014	.022	-.073	-.624	.535
	WidthDiff	.080	.108	.089	.736	.464
	OLDiff	.184	.136	.181	1.348	.182
	OWDiff	-.164	.182	-.125	-.900	.372
	HHDiff	-.053	.111	-.066	-.477	.635
	WHDiff	.192	.081	.317	2.369	.021
	InqDiff	.024	.030	.095	.811	.420
2	(Constant)	4.702	1.164		4.041	.000
	LengthDiff	-.012	.022	-.066	-.553	.582
	WidthDiff	.076	.110	.085	.696	.489
	OLDiff	.182	.138	.179	1.321	.191
	OWDiff	-.161	.184	-.122	-.874	.386
	HHDiff	-.056	.112	-.070	-.502	.617
	WHDiff	.189	.082	.313	2.302	.024
	InqDiff	.023	.030	.092	.777	.440
	%RedDiff	-.005	.019	-.032	-.260	.796

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a. Dependent Variable: PreyDiff

Do pitchers that differ more in hood width differ more in prey capture?

There is significant positive correlation between difference in prey type captured and difference in hood width (R^2= 0.066, d.f. =74, p=0.024: Figure 5). This result suggests that pitchers that have more different hood width sizes will capture more different types of prey. Pitchers that are more similar in hood width will capture more similar types of prey (Figure 5).

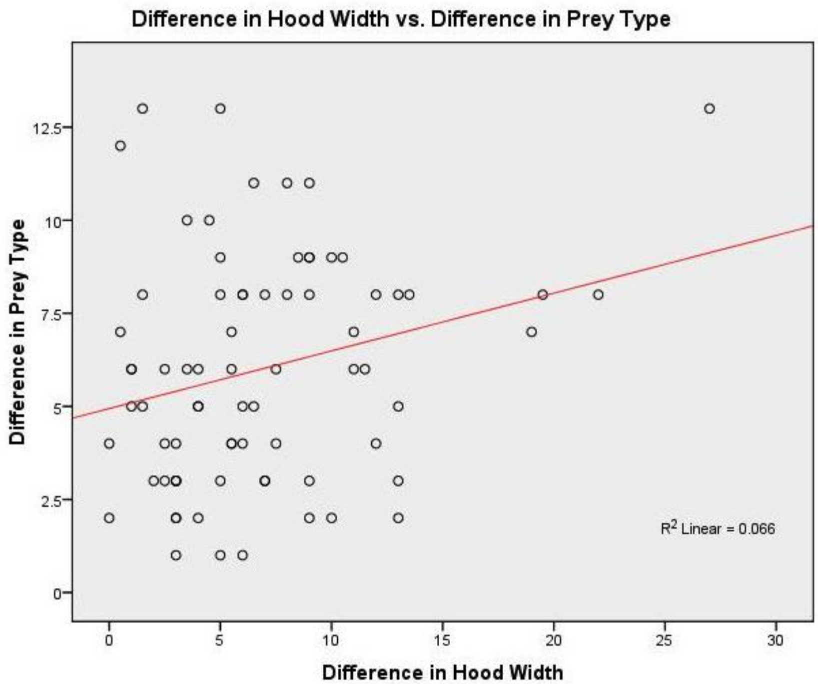

Figure 5: Figure 5 displays a significant positive relationship between prey type differences and hood width differences. Each point represents a pair of pitchers on the same plant.

Do pitchers that differ more in trichome density differ more in prey types captured?

We regressed hair density against difference in prey types separately because of the small sample size used for trichome density. Difference in prey types captured is not a function of hair density differences. There is a not a significant relationship between trichome density and variation in captured prey types (R^2= 0.069, d.f.=8, p>0.4: Figure 6).

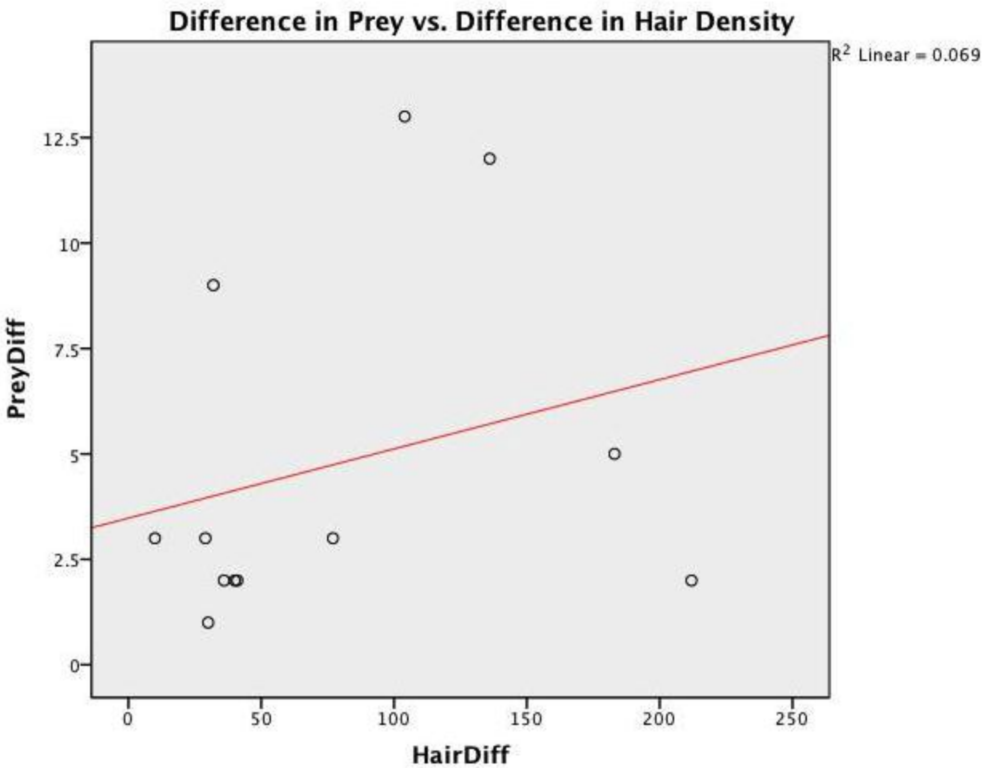

Figure 6: Figure 6 shows a weak positive correlation between prey type difference and hair density. Each point represents a pair of pitchers on the same plant.

Discussion

Based on the paired t-test, simple regression, and multiple ordered regression, we found that color was not used as a mechanism to partition prey resources within an individual plant (Figures 3, 4). After factoring out the effects of hair density, pitcher size, aperture size, and hood size, our results suggest that there is not a relationship between magnitude of redness and magnitude of the difference in prey types captured. Pitchers that are more similar in color do not capture more similar prey than pitchers of different color on the same plant. However, we suspect that resource partitioning is occurring through other techniques.

Hood Width

The results of the multiple regression suggest that pitchers may use hood width as a method to partition prey resources (p=0.024: Table 1). We wondered how this adaptation would help pitcher plants partition prey resources and why this strategy is more beneficial than color. Several other studies suggest that hood width does play a role insect capture (Cresswell 1998, and Newell and Nastase 1998). These studies suggest that larger hoods are able to capture bigger insects and a larger quantity of insects. Their results do not however, explain the variation in hood width across pitchers of the same plant.

How could hood width help partition prey resources?

In order to determine how hood width could help partition prey resources, we used 50 pitchers with the 25 largest hood widths and 25 pitchers with the smallest hood widths. We divided the insects present in these pitchers into 15 categories based on the most abundant types. If an individual species had more than 10 individuals, it was given its own category. Using the partial Chi-squared values from a Chi-squared analysis, we determined which prey types were contributing the most to the total Chi-squared value (Table 2). We determined that prey types with a partial Chi-squared sum greater than 2.0 were disproportionately represented in pitchers with either larger or smaller hoods. Prey that was overrepresented in pitchers with larger hoods included Chironomid midges, flies, and Myrmecinae ants. Prey that was disproportionally represented in pitchers with smaller hoods included two types of mites, ants, and beetles.

It is possible that pitchers with larger hoods capture more flying insects than pitchers with smaller hoods because there is more surface area for a flying insect to become trapped on. It is also plausible that smaller hooded pitchers capture more crawling insects because there is a smaller distance to climb before falling into the pitcher opening. Complimentarily, Newell and Nastase (1998) found that pitchers closer to the ground captured a smaller proportion of flying insects. Following this logic, with less distance to travel, there is a slighter chance that crawling insects could fall off the pitcher before falling into the trap. Similarly, there is a smaller chance that another predator could capture the insect before it landed in the pitcher.

Table 2: Table 2 features the observed, expected partial Chi-squared values that were used to determine which prey types were disproportionately found in pitchers with larger and smaller hood widths. Larger partial Chi-squared values indicate that a particular prey type is contributing more to the overall Chi-squared value.

Insect type		Small Width	Large Width	Partial X^2 Sum
Other Mites	Observed	5	6	
	Expected	4.4	6.6	
	Partial X^2	0.082	0.055	0.136
Mite 2	Observed	13	4	
	Expected	6.7	10.3	
	Partial X^2	5.924	3.853	9.777
Mite 3	Observed	12	8	
	Expected	7.9	12.1	
	Partial X^2	2.128	1.389	3.517
Mite 6	Observed	9	7	
	Expected	6.3	9.7	
	Partial X^2	1.157	0.752	1.909
Scuttle and Gnat Flies	Observed	1	4	
	Expected	2	3	
	Partial X^2	0.5	0.333	0.833
Other Flies	Observed	1	14	
	Expected	6	9	
	Partial X^2	4.167	2.778	6.944
Wasps	Observed	1	4	
	Expected	2	3	
	Partial X^2	0.5	0.333	0.833
Midges	Observed	1	11	
	Expected	4.8	7.2	
	Partial X^2	3.008	2.006	5.014
Mosquitos	Observed	5	9	
	Expected	5.6	8.4	
	Partial X^2	0.064	0.043	0.107
Muscoid Flies	Observed	2	8	
	Expected	4	6	
	Partial X^2	1	0.667	1.667
Myrmecinae Ant	Observed	2	10	
	Expected	4.8	7.2	
	Partial X^2	1.633	1.089	2.722
Ant 18	Observed	5	2	
	Expected	2.8	4.2	
	Partial X^2	1.729	1.152	2.881
Other Ants	Observed	9	18	
	Expected	10.7	16.3	
	Partial X^2	0.270	0.177	0.447
Spiders	Observed	4	5	
	Expected	3.6	5.4	
	Partial X^2	0.044	0.030	0.074
Beetles	Observed	3	1	
	Expected	1.6	2.4	
	Partial X^2	1.225	0.817	2.042
			Total:	38.905

Why could hood width be more advantageous to partition prey resources than color?

Using hood width to partition prey resources could be a better strategy than using color because it is possible that pitchers exhibit phenotypic plasticity (Gill *et al.* 2011). If pitchers were to change color as a function of prey capture, all pitchers on an individual plant could look the same at given times based on amount of prey captured. If pitchers on the same plant look the same, then using color as a mechanism of resource partitioning would be ineffective. Hood size would be a more effective tool for resource partitioning because even if color changes periodically, size remains constant. It is a characteristic that can be controlled by the plant rather than manipulated by the environment and resource intake, like color.

Similarly, hood width may be a more efficient way to partition resources at night. At night, when visibility is limited, size would be a more effective in leading to the capture of insects than color. Size is a characteristic that remains constant throughout the entire day whereas color is only effective for part of the day. Insects that fly or are active at night are more likely to be affected by size than by color. Some literature suggests however, that some insects have excellent vision at night and are able to easily navigate obstacles (Warrant and Dacke 2010).

Other Factors to Consider and Future Experiments:

It is important to consider that the positive relationship seen between hood width and difference in prey types captured may not have been as strong as it is in nature based on our experimental design. When selecting samples, we intentionally chose plants that had two pitchers of similar color and one pitcher with different color. Because we intentionally tried to standardize size and statistically factor out size variants that could be masking the effect of color on prey capture, we do not have a truly representative sample of varying hood widths. Had we intentionally chosen pitchers that were dramatically different in hood width we may have seen a stronger correlation. This is a possible area of future study.

It is also possible that the relationship between hood width and prey types captured might get stronger as time passes because pitcher plants are constantly growing and creating new pitchers throughout their growing season. Growth of new leaves may yield a greater variation in hood width across pitchers on the same plant. Since we only sampled during a brief period in the spring, we are unable to quantify the variation that could occur as time passes and new pitchers grow. Extending the length of our study and sampling the pitchers more than once throughout the summer may give a more accurate result of resource partitioning of prey resources by hood width. Moreover, testing the variation in pitcher hood width across all pitchers on an individual plant against the variation in hood width seen by choosing random pitchers on the same plant could also reveal if resource partitioning is occurring based on hood width. If the variation across all of the pitchers on a single plant is greater than the variation occurring just by chance, then hood width is being used a mechanism of resource partitioning.

It is plausible that pitcher plants could partition resources based on nectar rather than appearance (Bennett and Ellison 2009). For example, pitchers on the same plant may differ in amount and types of nectar used to lure different types of insects and thus maximize prey capture. Testing nectar as a mechanism of resource partitioning was out of the scope of this study. Measuring the amount of nectar produced by each pitcher, evaluating the nectar type produced by each pitcher, and/or manipulating the nectar of each pitcher may be useful in future experiments that examine possible resource partitioning occurring in *S. purpurea*.

UV patterns could also be acting as a mechanism as resource partitioning. It has been suggested that insects are attracted to UV light (Craig and Bernard 1990). Perhaps pitchers on an individual plant exhibit different UV patterns on their hoods that attract different types of insects. Although, like nectar, we were unable to test this variable, it is a factor that could be tested in future experiments.

Although our results suggest that pitcher plants do not use color as a tool to partition prey resources in order to maximize prey capture, it is still premature to completely reject our original hypothesis. Because pitcher color may be plastic, the color that we witnessed during the sampling period may not actually be the colors that affected insect capture. The prey that we examined in the sampled pitchers may have been in the pitcher for over a month. There is a disconnect between the time of actual insect capture and the sampling period. If pitcher color does change as a function of prey capture, we would lose the relationship between color and prey types captured by the time that we sampled the pitchers.

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