THE RELATIONSHIP BETWEEN PREY CAPTURE AND CHARACTERISTICS OF THE CARNIVOROUS PITCHER PLANT, *Sarracenia alata* WOOD

by

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INTRODUCTION

Carnivorous plants inhabit sites characterized by high light, abundant water, and low nutrients (Givnish et al. 1984, Benzing 1987). In these habitats, nutrients are supplemented by using modified leaves to trap, digest, and assimilate minerals from animal (usually insect) prey (Schnell 2002, Juniper *et al.* 1989). The absorption of nitrogen and phosphorus from prey has been reported to increase the biomass, growth rate, vegetative propagation, and sexual reproductive success of carnivorous plants (e.g., Aldenius *et al*. 1983, Gibson 1983, Thum 1988, Zamora *et al.* 1997).

Prey capture varies widely within and among populations of carnivorous pitcher plants (Wolfe 1981, Cresswell 1991, 1993, Heard 1998). There are several potential explanations for this variation. Among these explanations is the variation in plant characteristics, such as coloration and nectar production, which have long been thought to serve as prey attractants (Givnish 1989, Juniper *et al*. 1989, Cresswell 1993).

The relationship between prey capture and plant characteristics has been examined in the purple pitcher plant, *S. purpurea*. Cresswell (1993) found that the biomass of prey captured was significantly related to the size of the pitcher, and the numbers of prey captured were significantly related to indices of variation in pitcher size, pigmentation, and available nectar. Heard (1998) corroborated that larger pitchers captured significantly more prey than smaller pitchers. However, pitcher size explained only 3.5% of the variation in prey capture. Newell and Nastase (1998) demonstrated that potential prey were more likely to visit pitchers with more red coloration. However, there was no correlation between the number of potential prey visiting a pitcher and pitcher age, length, or mouth width.

These inconsistent results suggest that plant characteristics associated with prey capture are still not well understood. This study examines the relationship between prey capture and plant characteristics such as size, coloration, and nectar in the pitcher plant, *Sarracenia alata* Wood.

MATERIALS AND METHODS

Study Organism

Sarracenia alata Wood is a rhizomatous, perennial herb that inhabits bogs along the Gulf coast states. It flowers from early March into April, and is largely senescent during the winter months. The range of *S. alata* can be divided into two zones: an eastern portion covering the coast of Mississippi and eastern Alabama, and a western portion extending from western Louisiana across the Sabine River into eastern Texas (Schnell 2002).

Sarracenia alata belongs to a group of carnivorous plants known as "pitcher plants." These plants are so named because their leaves form a hollow tube, or pitcher. These pitcher-shaped leaves provide both energy through photosynthesis and minerals through carnivory. The tip of the leaf forms a flap, or "hood," that extends over the pitcher opening, but does not occlude it. The "rib," which runs the length of the pitcher, is the region where the two sides of the leaf meet to form the tube. At the top of the pitcher, surrounding most of the opening, is a swollen portion of tissue called the "lip." Nectar is commonly found on the hood, lip, and rib of the plant (Joel 1986, Juniper *et al.* 1989). This nectar is believed to serve as an attractant for insects (potential prey) visiting the plant (Juniper *et al*. 1989). Red coloration and UV patterns found on the hood might also serve as a signal to potential prey that there is a source of nectar (Juniper *et al.* 1989).

Once an insect arrives at a pitcher, the inner waxy surface near the opening makes it difficult for the insect to maintain its footing. After falling into the pitcher, downward pointing hairs prevent the escape of the insect. The prey item is then digested by a combination of enzymes secreted from the cells of the pitcher wall and the activity of commensal insects, usually larvae of sarcophagid flies and the mosquito genus *Wyeomyia* (Schnell 2002, Juniper et al. 1989). Then mineral nutrients, mainly nitrogen and phosphorous compounds, are absorbed by the plant (Plummer and Kethley 1964, Christensen 1976, Chandler and Anderson 1976).

The success of the pitchers is diminished by the presence of the noctuid moth, *Exyra semicrocea*. The larvae of this moth reside in the pitcher, feeding on the plant tissues and girdling the wall so that the pitcher often collapses, protecting the larvae from its predators (Schnell 2002). If the pitcher does not collapse, the larvae will spin a web of silk near the opening, preventing any further prey capture for the pitcher (Jones 1907). The larvae emerge from pupae in the spring after overwintering in the pitcher (Jones 1907). The presence of *E. semicrocea* in a pitcher effectively kills the pitcher, and it is not uncommon for nearly all of the pitchers in our sites to be infested by the end of the summer (personal observation).

Field Methods

The pitchers were selected from three sites in Kisatchie National Forest, Louisiana (~31º30'N, 93º4'W). The first of these bogs (known locally as Hooker bog and hereafter as "Site A") is a depression bog. Middle Branch bog (hereafter, "Site B") and Sulfur Springs bog (hereafter, "Site C") are hillside seepage bogs. On 10 April 2004, four 5-m transects were laid in each of the three sites. Every 20 cm, we attached a white tag to the rib of the closest young pitcher (either newly opened or on the verge of opening). Pitchers of the same age were selected to avoid age-related differences in prey capture (Fish and Hall 1978). A small piece of cotton

was gently pushed down into each of the open pitchers. This marked the beginning of our study and allowed us to exclude any previous prey capture from our analyses. Pitchers that were on the verge of opening did not receive a cotton plug.

Plants were sampled and prey were collected on 13 May 2004. All pitchers that had not fallen horizontal and had not been attacked by *Exyra* were collected. The height of the pitcher (distance from the substrate to the lip along the rib) and funnel diameter were measured to the nearest mm. We then took samples of nectar from the pitcher by modifying the method of McKenna and Thomson (1988). We dampened a 1-cm^2 piece of filter paper with DI water and placed it on the rib of the pitcher (a few centimeters below the lip) for five seconds. The filter paper was then placed in a screw-cap vile for storage until it could be returned to the lab and dried. Nectar sampling was repeated for the lip, top of the hood, and bottom of the hood. The hood of the pitcher was then cut horizontally in line with the lip, and placed in a snap-cap vial for analysis of red coloration (see below). Each pitcher was then cut and placed with its contents into snap-cap vials.

Inclement weather prevented the collection of all pitchers on the same day. Therefore, half of the pitchers in Site A were allowed to capture for 33 days. The remaining half was collected after 35 days. The pitchers in Site C were allowed to capture for 36 days and the pitchers from Site B remained for 37 days.

Analysis of Prey Capture

Upon return to the lab, the snap-cap vials containing the pitchers and their contents were filled with a 70% (aq) ethanol solution for preservation. The pitcher contents were sorted using a dissecting microscope into four categories: intact ants, intact flying insects, unidentifiable matter (primarily insect exoskeletons, hereafter “detritus”), and commensal insects. Commensal

insects were excluded from the prey capture because they cannot be digested by the pitcher plants. Counts were also obtained for both intact ants and intact flying insects. Additionally, the intact insects of 26 randomly selected pitchers were identified to order, counted, and weighed.

The sorted contents were then dried to constant mass at 50ºC for at least three full days. The contents of each pitcher were weighed by category to the nearest 0.1 mg. When samples had a negligible mass, a mass of 0.01mg was assigned. In order to account for the differences in the number of days the pitchers were open, total mass of prey captured and mass of detritus were reported as total mass per day and mass of detritus per day.

Analysis of Coloration

The pitcher hoods were scanned in color with a scale bar at a resolution of 600 dots per inch using the HP scanjet 4570c. Analyses of total hood area and area of red coloration was performed on a Medion AkoyaEX computer using the public domain NIH Image program (developed at the U.S. National Institutes of Health and available on the internet at http://rsb.info.nih.gov/nih-image/). In order to use NIH Image, the hood images were converted to gray scale. By adjusting the contrast threshold for each hood image, we were able to make the entire hood appear black. The black area was then selected and measured to obtain the hood area for each pitcher. After this, the threshold was increased by 70 shades so that only the red coloration appeared black. The difference of 70 shades provided the best contrast between the red coloration and the green hoods. Comparison with the original color images indicated that this method for selecting the upper threshold did capture the areas of red coloration quite accurately. The black area, which represented the area of red coloration, was then selected and measured. From the measurements of hood area and area of red coloration, a percentage of red coloration was obtained.

Analysis of Nectar Samples

Upon return from the field, the nectar samples were dried in an oven at 50ºC for 3 days, sealed in their screw-cap vials, and stored at room temperature. In order to redissolve the sugars for analysis, three ml DI water were added to the screw-cap vial containing the wick. The wick sat in contact with the water for ten minutes before one ml of the nectar solution was removed for use in the anthrone colorimetric technique (Cresswell 1993). Because this technique is based on comparison to a sucrose standard curve, the units are reported in µg sucrose equivalents per milliliter (µgSE/ml) for each of the nectar samples.

Statistical Analyses

In order to assess differences among sites, analyses of variance were performed on prey capture and pitcher characteristics. Correlation matrices revealed the relationships between the various plant characteristics (height, funnel diameter, hood area, percent red coloration on hoods, and nectar). Stepwise regressions were used to determine the factor(s) related to prey capture (measured by total mass, mass of intact insects, and mass of detritus). The independent variables in the analyses were hood area, percent hood area occupied by red coloration (arcsine-transformed), and bottom, lip, rib, and top nectar. In all analyses, a significance level of 0.05 was used.

RESULTS

Differences between sites

Compared to Sites B and C, the population at Site A had significantly smaller pitchers (in height, funnel diameter, and hood area), possessed significantly lower values for detritus per day, and captured significantly less total mass per day (Table 1; Figure 1). Because there were

significant differences among sites in plant characteristics and prey capture, the sites were separated for the remainder of the analyses.

Relationships between plant characteristics

Indices of pitcher size (height, funnel diameter, and hood area) were highly significantly correlated among plants within a site (Tables 2-4). There was a significant correlation between rib nectar and top nectar in Sites A and B (Tables 2 and 3). In the pitchers of Site C, there also were significant correlations between top and bottom nectar and between top and lip nectar (Table 4). There was a negative correlation between coloration and indices of pitcher size, but this relationship was only significant for funnel diameter in Site A. Other correlations between pitcher characteristics were not statistically significant.

Prey capture

Hymenoptera, Diptera, and Coleoptera accounted for 85% of the intact prey numbers in the 26 randomly selected plants, with Lepidoptera, Hemiptera, and Homoptera completing the remaining 15% (Table 5). Exlcuding ants, hymenoptera made up 66.5% of the prey capture by weight, followed by Hemiptera, Diptera, Lepidoptera, and Coleoptera.

When all pitchers were considered, ants accounted for 97.0% of the number of intact insects found in Site A. They accounted for only 42.3% of the intact insects in Site B, and 81.7% of the intact insects in Site C. However, Kruskal-Wallis analyses indicated that there were no significant differences between sites in the number of intact ants, numbers of other intact insects, or the total mass of intact insects captured.

Relationships between prey capture and plant characteristics

In site A, hood area was the best determinant of total mass captured per day, whereas in Site B, height had the strongest influence (Table 6). In Site C, total mass captured per day was

strongly affected by hood area, but there was also a significant contribution by bottom nectar and rib nectar (Table 6).

The mass of detritus per day was most strongly influenced by hood area in Site A and height in Site B (Table 7). In Site C, hood area explained the most variation in mass of detritus per day, with bottom nectar also making a significant contribution (Table 7).

There was no significant relationship between pitcher characteristics and the total mass of intact insects in any of the sites. There were also no significant relationships between the number of intact insects (other than ants) and the pitcher characteristics. There was a significant relationship between the number of intact ants in Site C and lip nectar ($r^2 = .569$, $P = .045$).

DISCUSSION

We found that there were significant differences in pitcher characteristics among populations. The population in Site A was significantly smaller in all indices of size, had the lowest average concentrations of lip and top nectar, and had the highest percentage of hood coloration. Site A, a depression bog, has soil consisting of a thick organic slurry, and is kept saturated by drainage from surrounding areas of greater elevation. Sites B and C are hillside seepage bogs in which water moves downslope through a layer of sandy soil. All three sites had minimal overgrowth due to controlled burns during the 2003 growing season and had abundant water. Though the bogs appeared to be similar, the differences in pitcher characteristics could be attributed to microclimate differences.

Genetic differences among the populations might also be responsible for the observed differences among sites in pitcher characteristics. The sites are relatively isolated from each other (A and B are approx. 2.5km apart, B and C are approx. 12.5km apart, and A and C are

separated by approx. 15km). Thus, genetic exchange between populations is potentially limited. At the moment, we are unable to separate the effects of habitat and genotype, but reciprocal transplant experiments might reveal the reasons for the differences among populations.

In addition to differences among the populations in pitcher characteristics, there were also significant differences in prey capture. The pitchers at Site A captured significantly less than the other two populations. The lower prey capture in Site A might be a result of the differences in pitcher characteristics or a difference in prey availability. However, Kruskal-Wallis analyses indicated that there were no significant differences between sites in the number of intact insects or in the numbers of orders found in each site. Thus, we have no evidence to support the latter explanation.

The amount of variation in prey capture explained by pitcher characteristics differed among sites. Height and hood area were significantly positively related to total mass of prey capture per day and mass of detritus accumulated per day in all populations. However, the amount of variation in prey capture explained by pitcher characteristics in Site B was much lower than in sites A and C. This could indicate that the pitcher characteristics influencing prey capture vary from site to site or that pitcher characteristics other than those measured had an influence on prey capture in Site B. It is also important to note that the slightly smaller sample size could be responsible for the greater variance and lower coefficients of determination in our analyses of Site B.

The number and mass of intact flying insects were not related to the pitcher characteristics of any population. This lack of relationship might be due to the high variance in the number and mass of intact insects among pitchers.

In Site C, the nectar samples from various locations on the pitcher were significantly related to mass of total prey captured per day, mass of detritus accumulated per day, and the number of intact ants. It is not immediately clear why this relationship exists only in Site C, but as mentioned earlier, it could simply be that the relationship between pitcher characteristics and prey capture varies from location to location.

Overall, our study indicates that pitcher size in *Sarracenia alata* is the most important factor in determining prey capture. However, it is still unclear whether the direct relationship between pitcher size and prey capture is due simply to a larger capture area in larger plants, a larger surface area of attractants such as nectar in larger plants, or both. Future studies might also explore the relationship between UV reflectance and prey capture.

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TABLE 1. - Summary of ANOVAs of pitcher characteristics and prey capture among sites

Trait	Source of Variation	*df*	*MS*	*F*	*P*
Funnel Diameter	Site	2	5.359	8.423	0.000
	Error	121	0.636		
Hood Area	Site	2	606.886	7.913	0.001
	Error	121	76.697		
Height	Site	2	2145.489	11.848	0.000
	Error	121	181.080		
Coloration[†]	Site	2	0.078	8.333	0.000
	Error	121	0.009		
Bottom Nectar	Site	2	62.022	3.058	0.051
	Error	117	20.284		
Detritus Per Day	Site	2	52.6328	9.381	0.000
	Error	89	5.610734		
Total Mass Per Day	Site	2	46.037	7.310	0.001
	Error	115	6.298		

[†] Coloration analyzed as arcsine-transformed % of hood area

TABLE 2. - Correlation matrix of pitcher characteristics in Site A (44 observations); values are Pearson's correlation coefficients (* indicates significance at $P \leq .05$, ** $P \leq .01$, *** $P \leq .001$)

	Height	Funnel Diameter	Hood Area	Coloration	Bottom Nectar	Lip Nectar	Rib Nectar	Top Nectar
Height	1							
Funnel Diameter	0.831***	1						
Hood Area	0.898***	0.908***	1					
Coloration†	-0.364	-0.502*	-0.474	1				
Bottom Nectar	0.444	0.200	0.273	0.179	1			
Lip Nectar	0.430	0.373	0.452	-0.335	0.215	1		
Rib Nectar	0.254	0.262	0.279	-0.048	0.285	0.456	1	
Top Nectar	0.347	0.334	0.305	0.124	0.407	0.245	0.597***	1

† Coloration analyzed as arcsine-transformed % of hood area

TABLE 3. – Correlation matrix of pitcher characteristics in Site B (31 observations); values are Pearson's correlation coefficients (* indicates significance at $P \leq .05$, ** $P \leq .01$, *** $P \leq .001$)

	Height	Funnel Diameter	Hood Area	Coloration	Bottom Nectar	Lip Nectar	Rib Nectar	Top Nectar
Height	1							
Funnel Diameter	0.534	1						
Hood Area	0.552	0.886***	1					
Coloration†	-0.523	-0.487	-0.514	1				
Bottom Nectar	-0.092	0.012	-0.314	0.059	1			
Lip Nectar	-0.021	0.126	0.034	-0.039	0.059	1		
Rib Nectar	0.206	0.267	0.148	-0.229	0.258	-0.062	1	
Top Nectar	-0.055	0.005	-0.094	-0.004	0.278	-0.152	0.568*	1

† Coloration analyzed as arcsine-transformed % of hood area

TABLE 4. - Correlation matrix of pitcher characteristics in Site C (38 observations); values are Pearson's correlation coefficients (* indicates significance at $P \leq .05$, ** $P \leq .01$, *** $P \leq .001$)

	Height	Funnel Diameter	Hood Area	Coloration	Bottom Nectar	Lip Nectar	Rib Nectar	Top Nectar
Height	1							
Funnel Diameter	0.746***	1						
Hood Area	0.797***	0.728***	1					
Coloration†	-0.334	-0.34	-0.456	1				
Bottom Nectar	0.177	0.054	0.363	-0.087	1			
Lip Nectar	0.228	0.17	0.336	-0.278	-0.015	1		
Rib Nectar	0.333	0.353	0.277	-0.267	-0.064	0.35	1	
Top Nectar	0.231	0.067	0.504	-0.208	0.534*	0.516*	0.199	1

† Coloration analyzed as arcsine-transformed % of hood area

TABLE 5. - Insect orders represented in 26 randomly selected pitchers (omitting ants, see text)

Taxon	# of prey	% of total
Hymenoptera	10	35.7
Diptera	8	28.6
Coleoptera	6	21.4
Lepidoptera	2	7.1
Hemiptera	1	3.6
Homoptera	1	3.6

TABLE 6. – Summary of stepwise regression of total mass per day on plant characteristics. Independent variables: height, hood area, funnel diameter, coloration†, bottom nectar, lip nectar, rib nectar, top nectar

Site	Step	Independent Variable Entered	Total r^2	Total *P*
A	1	Hood Area	0.756	0.000
B	1	Height	0.370	0.000
C	1	Hood Area	0.516	0.000
	2	Bottom Nectar	0.579	0.031
	3	Rib Nectar	0.633	0.034

† Coloration analyzed as arcsine-transformed % of hood area

TABLE 7. – Summary of stepwise regression of average mass of detritus per day. Independent variables: height, hood area, funnel diameter, coloration†, bottom nectar, lip nectar, rib nectar, top nectar

Site	Step	Independent Variable Entered	Total r^2	Total *P*
A	1	Hood Area	0.745	0.000
B	1	Height	0.486	0.000
	2	Hood Area	0.582	0.039
C	1	Hood Area	0.564	0.000
	2	Bottom Nectar	0.64	0.020

† Coloration analyzed as arcsine-transformed % of hood area

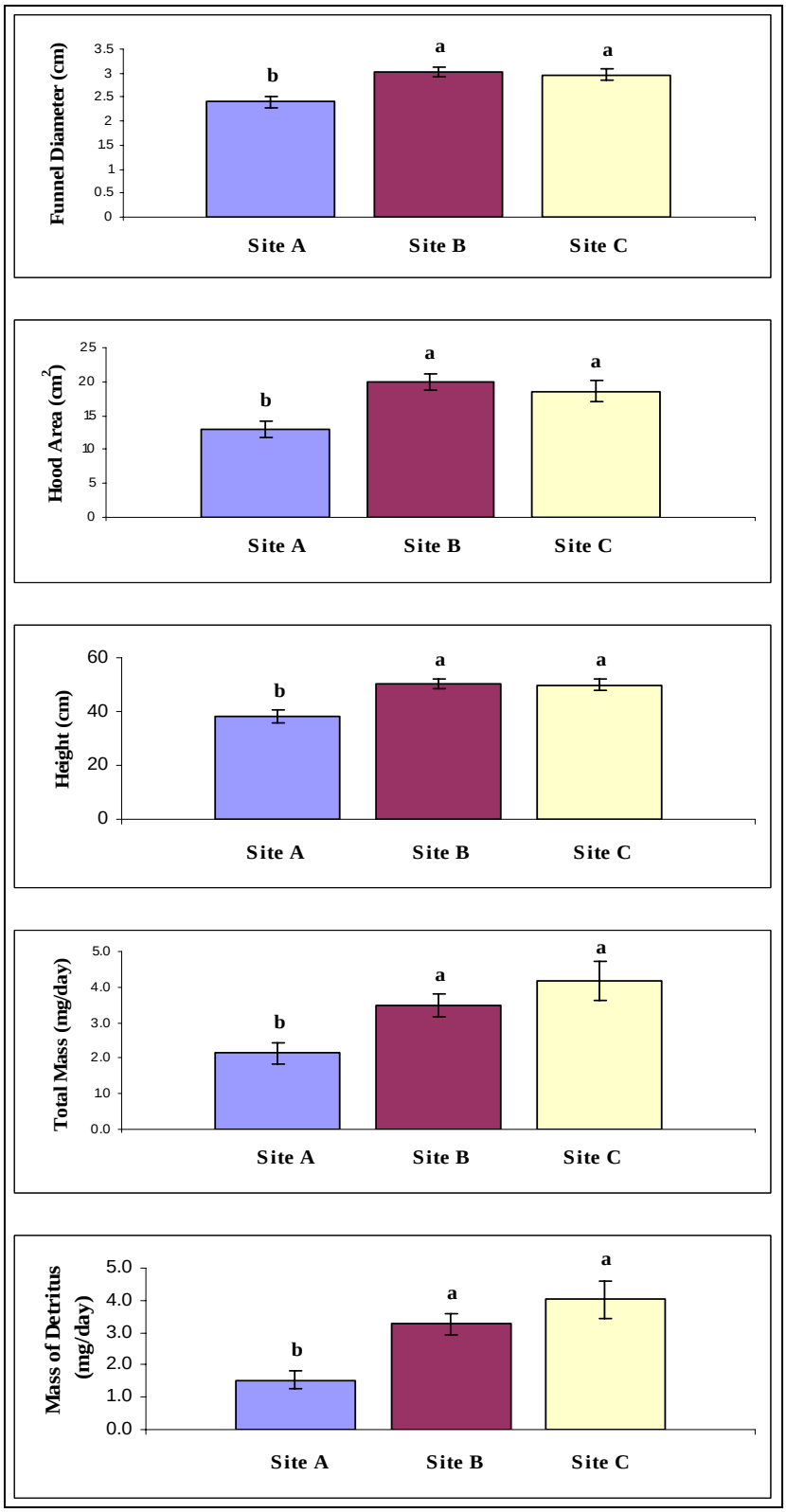

FIGURE 1. - Differences among sites in some pitcher characteristics and prey capture. Bars are means +/- 1 S.E. Different letters above bars indicate significant differences ($P \leq .05$)

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ABSTRACT

THE RELATIONSHIP BETWEEN PREY CAPTURE AND CHARACTERISTICS OF THE CARNIVOROUS PITCHER PLANT, *Sarracenia alata* WOOD

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We examined the relationship between pitcher characteristics and prey capture in three populations of the carnivorous plant *Sarracenia alata* Wood. The pitcher characteristics measured were nectar, coloration, and three indices of size. The indices of size (height, funnel diameter, and hood area) were highly correlated in all three populations. Pitcher size and mass of prey captured per day differed significantly among populations. Pitcher size was significantly positively related to total mass of prey capture per day, explaining 37-76% of the variation depending on the population. In one of the populations, nectar was also significantly related to prey capture per day. Pitcher coloration was not found to be significantly related to prey capture per day in any of the populations. These results indicate that the size of the pitcher is important in determining the amount of prey capture. Further research is needed to determine whether the direct relationship between pitcher size and prey capture is due simply to a larger capture area in larger plants, a larger surface area of attractants such as nectar in larger plants, or both. Future studies might also consider the relationship between prey capture and pitcher characteristics such as UV reflectance and volatile compounds.