An Examination of Insect Capture Capacities and Inquiline Larvae Communities in *Sarracenia purpurea* with respect to Pitcher Hood Morphological Adaptations

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Abstract

The purple pitcher plant (*Sarracenia purpurea*) requires both capture of prey insects to supplement nutrients from the nutrient-poor soil in which they live and inhabitation by Diptera larvae to digest these nutrients. We wish to determine if hood morphology in the purple pitcher plant has evolved to attract prey or to suit female mosquito (*Wyeomyia smithii*) and midge (*Metriocnemus knabi*) preferences for oviposition sites. We measured various aspects of hood morphology (height, width, opening width, surface area and opening area), and rated each pitcher on a scale of percent red coloration, and related each of these factors to number of captured prey, number of larvae, and biomass of all dry contents of the pitcher.

All components of pitcher hood size and opening were found to have a significantly positive relationship with inquiline larval populations, and greener pitchers had both a significantly higher proportion of larval populations and populations of significantly greater size than red pitchers. In contrast, the number of prey captured was not related to either pitcher morphology or color. We conclude that increased pitcher hood size and opening size, as well as greener pitcher color, are preferred by mosquito and midge females for oviposition sites, but these attributes do not increase prey capture success.

INTRODUCTION

Carnivory in plants is an interesting phenomenon thought to have evolved multiple times as a result of convergent evolution (Albert et al. 1992). This adaptation allows these plants to survive in environments which contain too few nutrients to satisfy the requirements of most other plants. Our study organism, the purple pitcher plant (*Sarracenia purpurea*), is a carnivorous plant that is the most widespread representative of its genus (Schell 1979) and occurs in low-nutrient environments such as bogs. The plant obtains supplemental nutrients by capturing insect prey in its specially adapted leaves (Cresswell 1993). These leaves are curled to form a pitcher-shape, which contains fluid (Cresswell 1993). The function of the hood (Fig. 1), an extension of the leaf beyond the opening, has not yet been determined with any certainty, but may serve to attract insect prey or ovipositing Diptera females (Cresswell 1993; Heard 1994).

Captured prey insects are partially digested for the plant by Diptera larvae which hatch and live within the pitcher's fluid (Bradshaw and Creelman 1984). In *S. purpurea*, mosquito (*Wyeomyia smithii*) and midge (*Metriocnemus knabi*) larvae increase the rate of ammonia production by feeding on and breaking down the pitcher's insect prey; nutrients in prey cannot be absorbed and used by the plant until they are released by feeding activities of inquiline organisms such as Diptera larvae (Heard 1994). This mutualistic relationship is essential for *S. purpurea* because the reduction of nitrogen to ammonia facilitates the manufacture and secretion of hydrolytic enzymes that are crucial for further digestion (Gallie and Chang 1997).

In *S. purpurea*, various morphological characteristics have been found to impact prey capture. For example, Cresswell (1993) found that greater biomass of prey was related to larger pitcher size, while a higher number of prey caught was related to larger pitcher size, more pigmentation, and more available nectar. Supporting some of Creswell's (1993) findings, Heard (1998) also found pitcher size to be a significant factor in the amount of prey captured. Newell and Nastase (1998) found that insect prey were more likely to visit pitchers with greater red venation as opposed to greener pitchers, but found general efficiency of capture (number of captures per number of visits) to be very low.

However, Heard (1998) found that pitcher size significantly accounted for a very small portion of insect capture rates (only 3.5%). In addition, Wolfe (1981) found that leaf size explained almost half of the variance in insect capture for older pitchers, but explained nothing about the variance in younger pitchers; instead, Wolfe (1981) found that younger pitchers, which tend to be green, capture more prey than older pitchers. Finally, Bennett and Ellison (2009) found that there was no relationship between red pigmentation and insect capture.

The relationship between pitcher morphology and inquiline larvae communities has also been investigated. Heard (1994) found that larger pitchers had more larvae than smaller pitchers, probably because they contained higher fluid levels (Nastase et al. 1995) and tend to catch more prey (Wolfe 1981; Cresswell 1993). Importantly, a pitcher's prey capture limits larval growth (Heard 1994). Larger pitchers are less likely to dry out in warmer temperatures, making them a safer habitat for larvae (Kingsolver 1979). Additionally, midge larvae facilitate mosquito growth (Heard 1994), and larger pitchers contain more midge larvae (Paterson and Cameron 1982).

We looked at the morphological traits in *Sarracenia purpurea,* specifically hood size and color variation, with respect to abundance of insect prey as well as Diptera larvae. We expected that larger hood size and larger hood opening size would both correspond to greater biomass of prey insects captured, as Cresswell (1993) found that a higher prey biomass corresponded to larger pitchers. Larger pitchers may reasonably be expected to have larger hoods. We also expected that green pitchers would capture greater prey biomass than would red pitchers, citing Wolfe's (1981) findings. We predicted that pitchers with larger hood size and hood opening size would contain greater numbers of inquiline larvae, because these pitchers would retain higher levels of fluid, which make them better habitats for Diptera larvae (Kingsolver 1979), and because larger pitchers tend to capture more prey (Cresswell 1993). Finally, we predicted that pitchers which are greener would contain greater numbers of inquiline larvae because green pitchers have been found to capture more insects (Wolfe 1981), and more insects translates into higher food supply for larvae.

METHODS

This study was conducted at Mud Lake Bog, part of the Little Traverse Conservancy's Wendy Oneil Memorial Preserve in Inverness Township, Cheboygan Co, near Pellston, MI (45° 36'N, 84° 36' W). Mud Lake bog is a quaking bog with an extensive *Sphagnum* mat, a good habitat for *S. purpurea*. We collected data on two separate days; measurement of hood dimensions occurred on the first day, and insect samples were collected on the second day. Insect samples were analyzed on subsequent days in the same week.

In this study we selected 25 pitcher plants. On each plant, we selected 3 pitchers which were open and not yet decaying (had no holes). For each pitcher, we measured hood width, hood height, and hood opening width (Fig. 1). Hood width was determined by lining the inner surface of the hood (at the level of the peristome) with string, marking the string where it met the ends of the hood, and measuring this distance with a ruler. Hood height was measured as the distance of the highest point of the hood above the level of the peristome. Hood opening width was measured as the width of the hood top opening along the peristome when looking down on the pitcher. Hood surface area and hood opening area were derived from the measurements we obtained. Hood surface area was determined by measuring the height and width of the hood and by calculating these values into a semicircle hood surface area. Hood opening area was determined by measuring the hood opening width and calculating the curved distance along the edge of the hood from its base to its highest point (1/4 of the perimeter of a circle), and multiplying these values to obtain the area of open space left between the hood's edges.

Each pitcher hood was also rated on a color scale running from 1 to 5 (1 = 0-20 % red, 2 = 21-40 % red, 3 = 41-60 % red, 4 = 61-80 % red, 5 = 81-100 % red). For our additional analyses of color variations, we grouped color scale 1 and 2 into "green" and color scale 4 and 5 into "red;" in this grouping, we disregarded scale 3, to avoid including pitchers which had roughly equal proportions of green and red coloration.

Additionally, for each pitcher we sampled captured prey using a 44.4 mL large-bulbed pipet and a smaller 5 mL pipet. Each pitcher was pipetted at least 3 times to ensure complete removal of all liquid. After removing the liquid, we examined the inner wall of each pitcher and removed any remaining insects with forceps. We placed each sample in a previously weighed 20 mL glass vial. The contents of each sample were then identified as prey insects or Diptera larvae. We counted fragments of insects as whole insects, due to the difficulty of identifying which insect different fragments may have come from originally. Each sample was then dried for 1 day in a 110° C oven. The empty weight of each vial was subtracted from the total weight of the vials after drying to obtain a measurement of overall biomass of the captured prey and larvae. Weight was measured in grams using a Mettler AE240–S analytical balance sensitive to 4 decimal places.

Statistical analyses were carried out using SPSS Statistics ver. 17. Correlation coefficients were calculated between larvae abundance and pitcher characteristics, between insect catch and pitcher characteristics, and between biomass and pitcher characteristics. We performed t-tests to determine the relationship between color group and larvae existence, and between color group and insect capture. To compare the means of number of larvae in pitchers of different color scale ratings and to compare the means of number of captured prey in pitchers of different color scale ratings, we carried out one-way ANOVA tests.

RESULTS

Linear regression analyses of our data showed significant positive relationships between five measures of pitcher hood morphological characteristics and number of Diptera larvae within the pitcher: pitcher hood opening area ($F_{0.05(1),1,65} = 26.244$, $p < 0.001$, $y = 0.02x – 0.13$, $R^2 = 0.288$; Fig. 2a); pitcher hood surface area ($F_{0.05(1),1,65} = 18.467$, $p < 0.001$, $y = 0.001x – .25$, $R^2 = 0.221$; Fig. 2b); pitcher hood width ($F_{0.05(1),1,65} = 19.649$, $p < 0.001$, $y = 0.13x – 3.87$, $R^2 = 0.232$; Fig. 2c); pitcher hood opening width ($F_{0.05(1),1,65} = 20.758$, $p < 0.001$, $y = 0.32x – 1.49$, $R^2 = 0.242$; Fig. 2d); and pitcher hood height ($F_{0.05(1),1,65} = 12.186$, $p = 0.001$, $y = 0.25x – 2.61$, $R^2 = 0.158$; Fig. 2e).

An independent samples t-test not assuming equal variances indicated that the presence of larvae was significantly related to red (N = 19) and green (N = 30) pitcher color groups (as described in our methods), with green pitchers containing more larvae on average than red pitchers ($t_{0.05\,(2),\,39.667} = 2.32$, $p = 0.026$; Fig. 3). A one-way ANOVA of our data showed that number of larvae were significantly related to pitcher rating on a color scale from green to red (1-5, as described in methods) ($F_{0.05\,(1),4,66} = 2.521$, $p = 0.049$), with greater numbers of larvae occurring in greener pitchers (Fig. 4). Additionally, significantly more green pitchers than red pitchers contained larvae ($t_{0.05\,(2),\,47} = 2.368$, $p = 0.022$; Fig. 5). However, nearly all of our “green” pitchers were category 2 (N = 29), while only one was from category 1 (N = 1).

Linear regression analyses of our data showed total dry biomass was not significantly related to hood opening area ($F_{0.05(1),1,69} = 0.048$, $p = 0.827$, $y = -4.488*10^{-7}x + 0.027$, $R^2 = 0.001$; Fig. 6a), hood surface area ($F_{0.05(1),1,69} = 0.322$, $p = 0.572$, $y = 9.532*10^{-7} + 0.023$, $R^2 = 0.005$; Fig. 6b), hood width ($F_{0.05(1),1,69} = 0.508$, $p = 0.478$, $y = 0.000x + 0.020$, $R^2 = 0.007$; Fig. 6c), hood opening width ($F_{0.05(1),1,69} = 0.140$, $p = 0.709$, $y = 0.000x + 0.028$, $R^2 = 0.002$; Fig. 6d), or hood height ($F_{0.05(1),1,69} = 0.041$, $p = 0.839$, $y = -6.986*10^{-7}x + 0.024$, $R^2 = 0.001$; Fig. 6e).

Linear regression analyses of prey capture and pitcher hood morphological characteristics produced no significant results. Number of insects captured had no significant correlation with hood opening area ($F_{0.05(1),1,69} = 0.355$, $p = 0.553$, $y = 0.004x + 3.187$, $R^2 = 0.005$; Fig. 7a), hood surface area ($F_{0.05(1),1,69} = 0.100$, $p = 0.752$, $y = 0.000x + 4.416$, $R^2 = 0.001$; Fig. 7b), hood width ($F_{0.05(1),1,69} = 0.005$, $p = 0.945$, $y = -0.004x + 4.141$, $R^2 = 0.000$; Fig. 7c), hood opening width ($F_{0.05(1),1,69} = 1.814$, $p = 0.182$, $y = 0.159x + 1.420$, $R^2 = 0.026$; Fig. 7d), or hood height ($F_{0.05(1),1,69} = 0.711$, $p = 0.402$, $y = -0.096*10^{-7}x + 6.348$, $R^2 = 0.010$; Fig. 7e).

In an independent samples t-test assuming equal variance, prey capture was found to be not significantly related with “green” (N = 30) or “red” (N = 19) categories ($t_{0.05\,(2),\,47} = -0.494$, $p = 0.623$; Fig.

8). In a one-way ANOVA, prey capture was similarly found to be not significantly related to pitcher color ($F_{0.05(1), 4, 66} = 0.875$, $p = 0.484$; Fig. 9).

DISCUSSION

Our data showing significant positive relationships between all five measures of pitcher hood morphology and number of larvae present suggests that mosquito females tend to lay eggs in pitchers which have hoods of larger size and which are more open. These characters may maximize the amount of fluid contained within the pitcher (Nastase et al. 1995), perhaps by maximizing trapped rainwater and/or minimizing evaporation(Kingsolver 1979); maximized pitcher fluid is a desirable condition for midge larvae because of a positive relationship between fluid volume and oxygen availability to larvae (Nastase et al. 1995; Cameron et al. 1977). Female midges selecting pitchers with more fluid will thus have higher offspring survival rates and consequently increased fitness. Since midge larvae facilitate mosquito growth (Heard 1994), this condition is also beneficial to mosquito larvae. Given that greater hood area is related to higher volume of fluid, and higher volume of fluid is related to several positive effects (the effects of higher oxygen levels [Cameron et al. 1977]) on larvae, greater hood area seems to have positive effects on inquiline larvae.

Our data show that a larger proportion of green pitchers than red pitchers tend to contain larvae, and green pitchers tend to have larger larvae populations than red pitchers. This indicates some preference exhibited by mosquito and midge females in egg-laying behaviors. It is important to note for all following analyses involving color that all but one (N = 29) of our "green" category pitchers belong to color scale 2, while only one (n N = 1) of our "green" pitchers belong to color scale 1. This should not negatively impact our analyses, because our grouping of colors into two distinct groups still shows the same relationship. Further studies should be conducted with larger sample sizes of different color categories to clarify this relationship. If these further studies find a very high average number of larvae in pitchers of color scale 1, this reinforces the pattern we observed. If they find a very low average number of larvae in pitchers of color scale 1, this may indicate that mosquito and midge females do not prefer the absolute greenest and youngest (Wolfe 1981) pitchers. Reasons to not prefer the youngest pitchers may be that they have not yet had time to accumulate enough prey to provide sufficient food for larvae. Alternatively, it might not be a function of preference at all. This pattern would also result if timing of Diptera female oviposition did not align properly with pitcher emergence and opening.

Mosquitoes may prefer greener pitchers in general for various reasons. Some studies have found that younger pitchers tend to be greener, and that older pitchers captured fewer prey insects

(Wolfe 1981); mosquitoes and midges may prefer to lay eggs in younger pitchers because they tend to have a greater chance of surviving long enough for the larvae to develop into adults, and increased food supply is good for larvae growth and survival (Istock et al. 1975). Many older pitchers were observed to have developed holes near the bottom which caused all or some fluid to drain, removing all captured prey and probably killing any larvae that the pitcher contained. Thus, mosquito and midge females preferring older pitchers would have offspring with a higher mortality rate and would thus be selected against.

Additionally, older pitchers have been found to catch fewer prey (Wolfe 1981), meaning younger pitchers are more successful at capturing prey, translating into increased food supply for larvae. Some evidence has been found associating an increased food supply with higher individual fitness (Istock et al. 1975), further increasing the fitness benefit of laying eggs in pitchers which capture more prey. Thus, mosquitoes and midges favoring younger pitchers for oviposition sites will be selected for. Since younger pitchers tend to be green (Wolfe 1981), and since larger pitchers probably also have larger hoods, this could mean that mosquitoes and midges preferring to lay eggs in green pitchers and pitchers with larger hoods would be inadvertently providing their young with more food and thereby increasing their survival rate.

Contrary to our findings relating presence of Diptera larvae and pitcher morphology, our data indicate no relationship between pitcher morphology and prey insect capture. However, it is important to remember the implications of our potential problems with color scale number 1 and sample size discussed above, though again this should not strongly impact our conclusions. Many other studies have investigated potential correlations between pitcher plant morphological characteristics and insect capture rates; yet the results of these studies were often mixed. Newell and Nastase (1998) found no significant correlation between number of potential prey visits and pitcher length or mouth width. Somewhat contrary to Newell and Nastase (1998), Cresswell (1993) found that larger pitchers capture more prey and larger prey items, translating into greater prey biomass. Expanding on Creswell's (1993) findings, Heard (1998) found that larger pitchers captured more prey biomass, but noted that size accounted for only a small portion of the variance. Most recently, Green and Horner (2007) found that pitcher size (measured by height, funnel diameter, and hood area, which were highly correlated) showed a significant positive relationship to prey capture. These results support Cresswell (1993) and Heard (1998) but not Newell and Nastase (1998), illustrating the contradictory findings of many contemporary studies regarding pitcher shape characteristics.

With respect to pitcher color, Newell and Nastase (1998) and Cresswell (1993) both found that prey were more likely to visit pitchers with greater red venation. On the other hand, Green and Horner (2007) found that coloration had no effect, illustrating disagreement about the relationship between color and prey capture as well. Our results which show no significant relationship between any measure of pitcher hood morphology and prey capture suggest another explanation for these previous disagreements about pitcher adaptations in relation to insect capture. Indeed, our findings suggest that pitcher characteristics function primarily to attract ovipositing mosquitoes and midges rather than insect prey.

We have previously discussed issues with pitcher color data, but there are other potential sources of bias in our study. First, a generally small sample size (made worse by a broken vial and a site destroyed between data collection days) may have influenced our findings. Second, the scale (Mettler AE240-S) used for measurement of biomass may not have been sensitive enough to detect the minute differences in weight. Finally, the measurement of biomass as an aggregate of prey insect and inquiline larvae samples could have been split into biomass of prey insects and biomass of inquiline larvae as two separate measurements; this was not done initially because larvae communities were not originally in the focus of our study, and were not added until after the drying of pitcher contents had occurred. Splitting the biomass measurement into these categories could have more strongly supported any conclusions we made about prey capture or larvae communities.

We conclude that increased pitcher hood size (measured by height, width, and area) and opening size (measured by opening width and opening width area), as well as greener pitcher color, are significantly related to higher inquiline populations of mosquito and midge larvae. These phenomena may be due to increased water retention (Nastase et al. 1995), increased prey capture (Cresswell 1993), or some other factor. Insect prey capture rates were found to not depend on either morphological or color characteristics. We conclude that pitcher hood morphology has evolved to attract ovipositing Diptera females rather than insect prey. This suggests an important mutualistic relationship between the *S. purpurea* and Diptera larvae specially adapted to live within the pitcher. Indeed, this relationship is at least partially obligatory mutualism. The benefit to each is so substantial that the survival of each is in serious question without the contribution of the other. This system displays factors which reinforce mutualism: lifelong associations and limited opportunities to receive these benefits elsewhere. Pitchers are dependent on the larvae for digestion of nutrients throughout their lives, while the larvae depend on the food and safe habitat provided by the pitcher (Bradshaw and Creelman 1984; Heard 1994). As the larvae are the top predators in the inquilines food chain within pitchers, their role in this food chain is essential in converting nitrogen into forms usable by the pitcher plant, which stimulates the production of hydrolytic enzymes by the plant which function in digestion (Bradshaw and Creelman 1984; Heard 1994). The strong mutualistic relationship between these two species suggests a significant coevolutionary relationship which may have many other aspects to be explored.

Additional studies should examine differential selection pressures on pitcher plants from mosquitoes and from midges. Also, other morphological characteristics of pitcher plants should be investigated in relation to larvae populations, such as overall pitcher size, pitcher volume, and keel width. Further studies may consider the effects of pitcher morphology on larvae growth rate, survival rate, and adult fitness. Further, it would be interesting to examine tropism (heliotropism, hydrotropism, thermotropism, thigmotropism, or others) in pitcher plant hoods; it is possible that pitcher plants are able to respond to changing weather conditions by changing the size of their opening to maximize fluid content to prevent evaporation and capturing precipitation at the appropriate times. Finally, microhabitat differences should be investigated for effects on pitcher morphology and/or mosquito or midge oviposition behavior differences.

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FIGURES

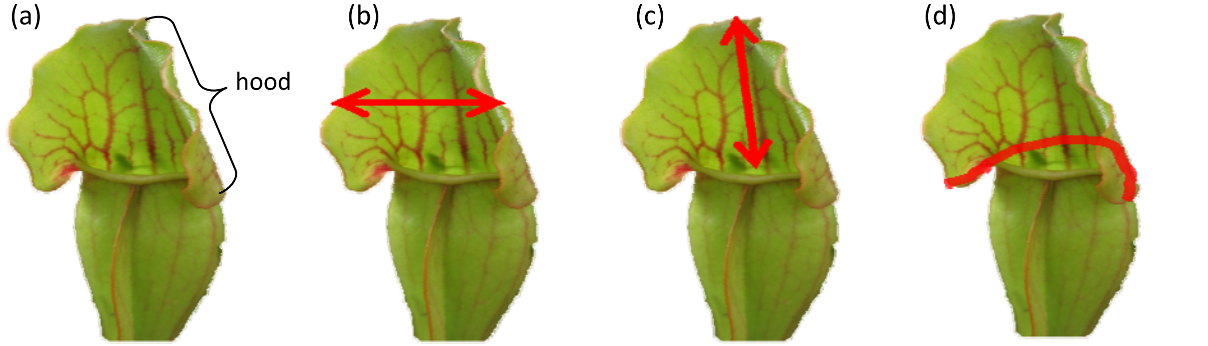


Figure 1. Diagram of pitcher morphology. Example pitcher, with hood indicated (a); hood measurements: hood opening width (b), hood height (c), and hood width (d).

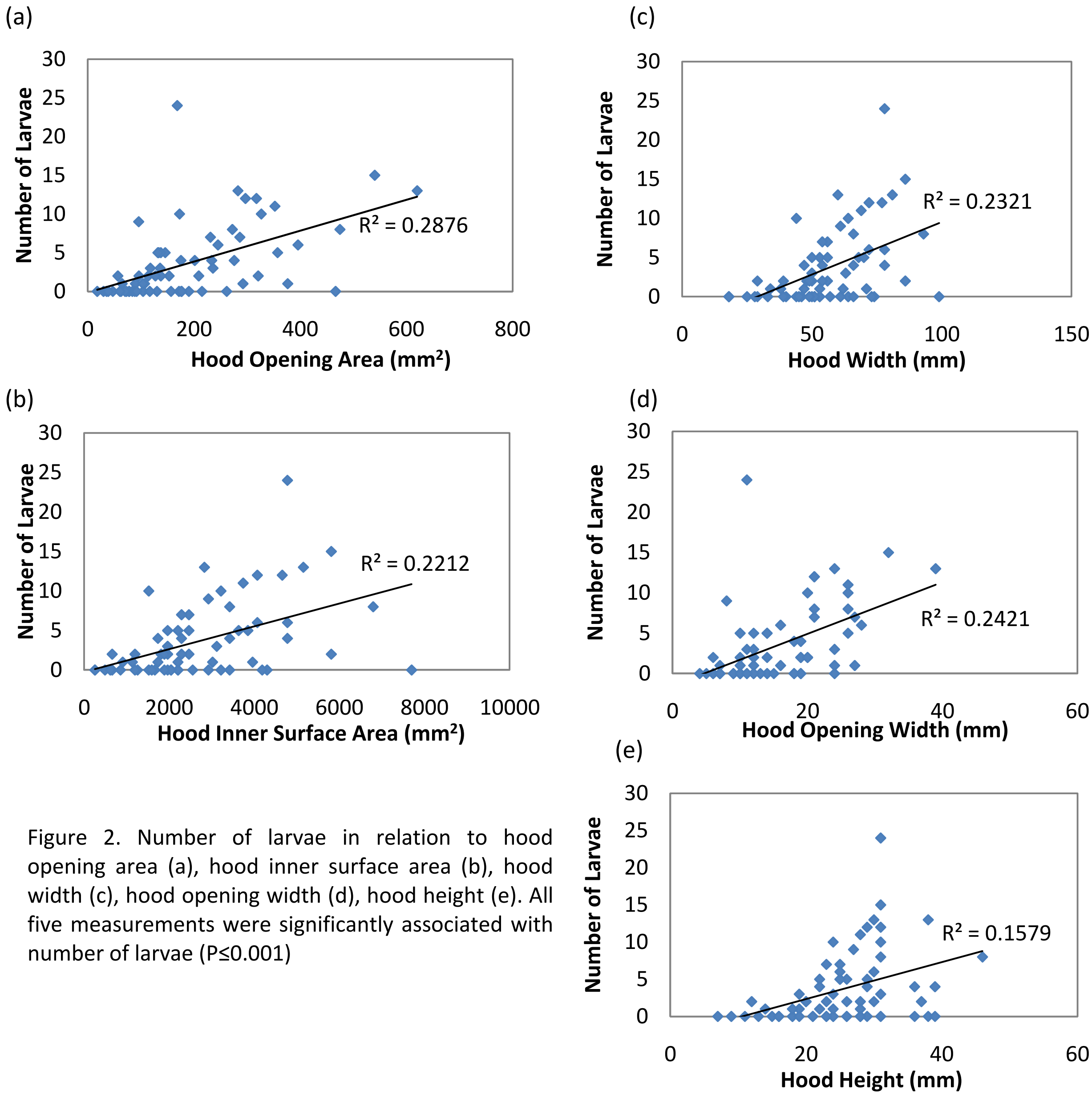


Figure 2. Number of larvae in relation to hood opening area (a), hood inner surface area (b), hood width (c), hood opening width (d), hood height (e). All five measurements were significantly associated with number of larvae ($P \leq 0.001$)

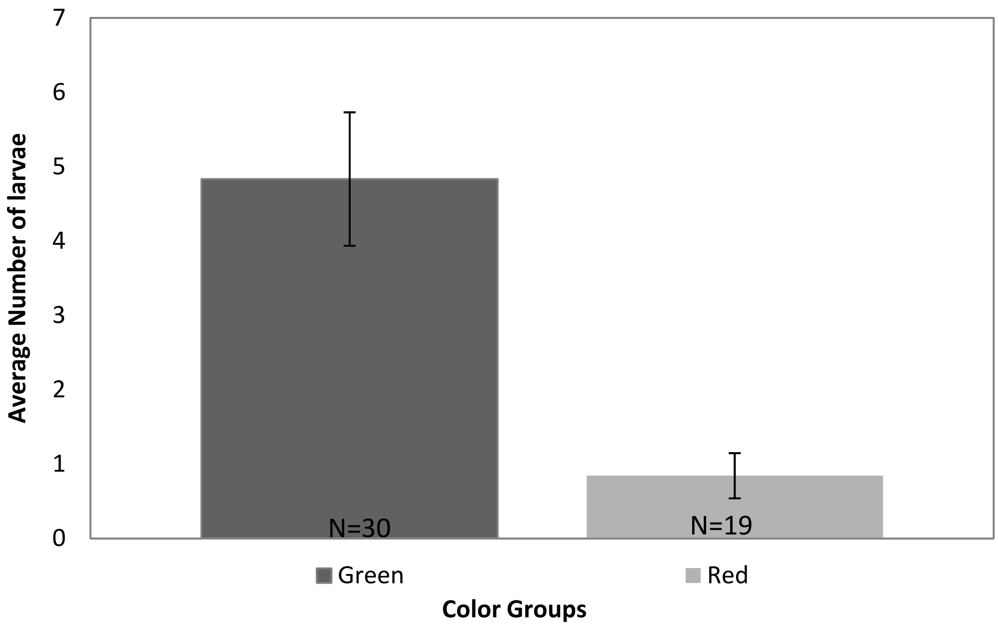


Figure 3. Average number of larvae (± SE) in *Sarracenia Purpurea* pitchers divided into color groups of “green” and “red”.

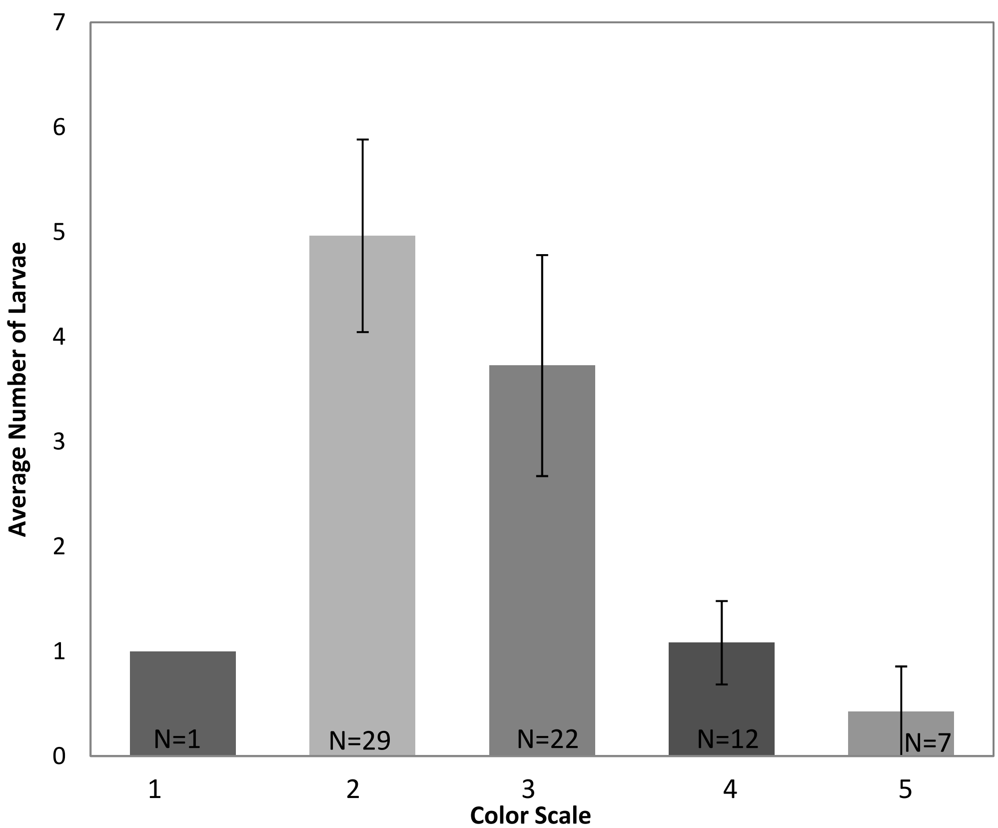


Figure 4. Average number of larvae (± SE) in *Sarracenia Purpurea* pitchers divided into a color scale of 1-5 (1 = 0-20 % red, 2 = 21-40 % red, 3 = 41-60 % red, 4 = 61-80 % red, 5 = 81-100 % red).

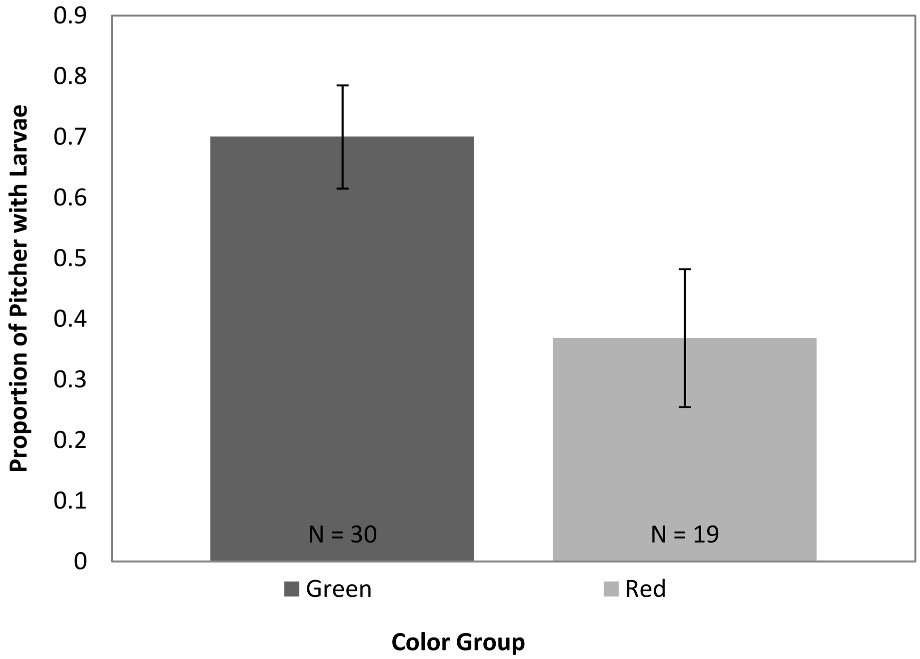
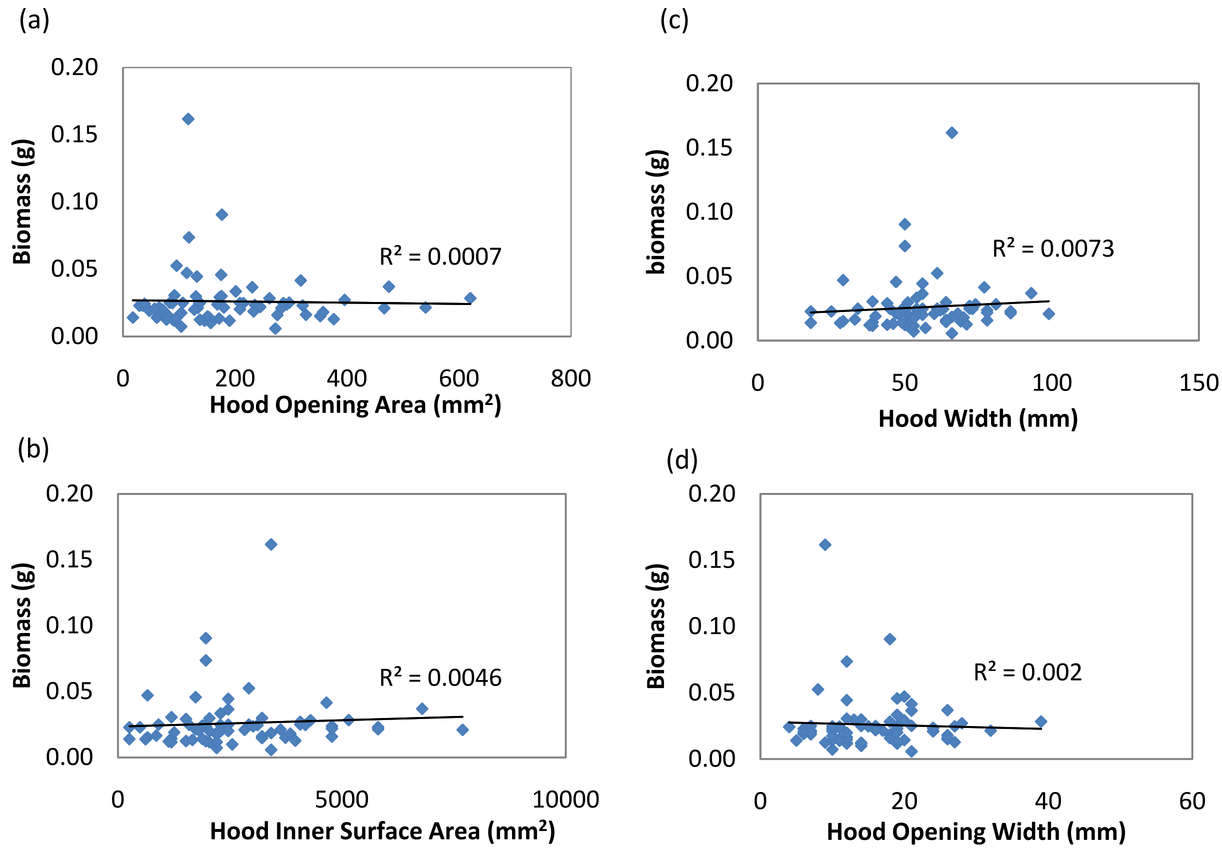


Figure 5. Proportion of *Sarracenia Purpurea* pitchers with larvae (± SE) divided into color groups of “green” and “red”.



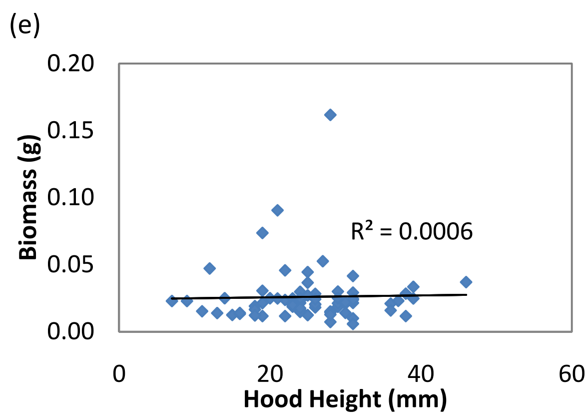
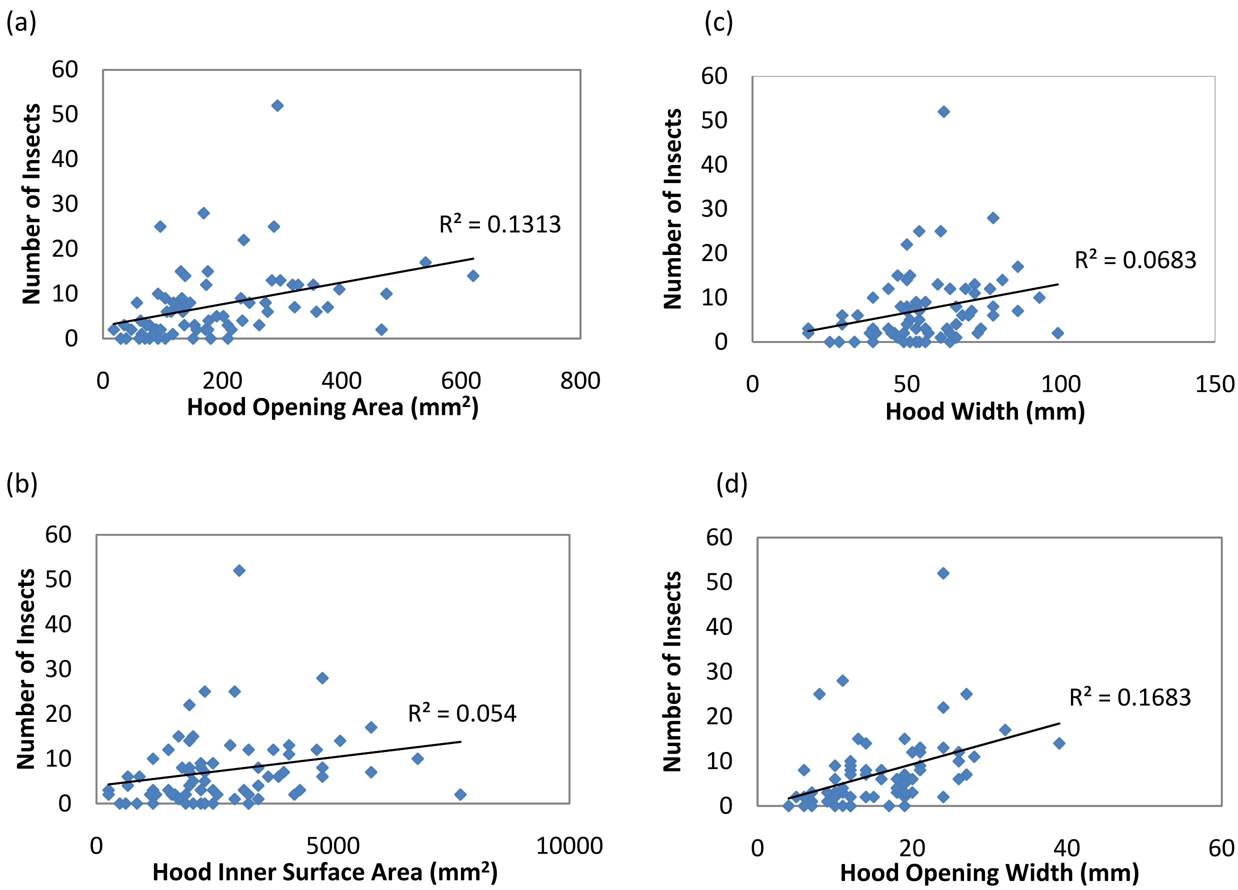


Figure 6. Dry biomass of insects and Diptera larvae in relation to hood opening area (a), hood inner surface area (b), hood width (c), hood opening width (d), hood height (e). All five measurements were not significantly associated with number of insects (P>0.05).



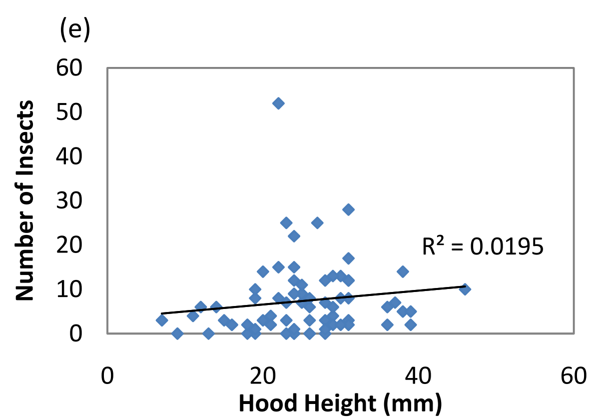


Figure 7. Number of insects in relation to hood opening area (a), hood inner surface area (b), hood width (c), hood opening width (d), hood height (e). All five measurements were not significantly associated with number of insects (P>0.05).

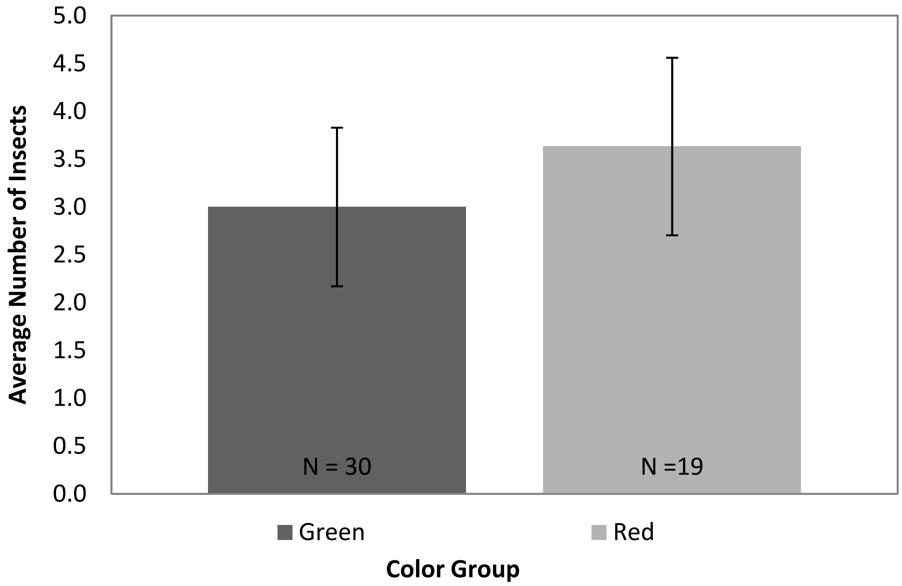


Figure 8. Average number of insects (± SE) in *Sarracenia Purpurea* pitchers divided into color groups of “green” and “red”.

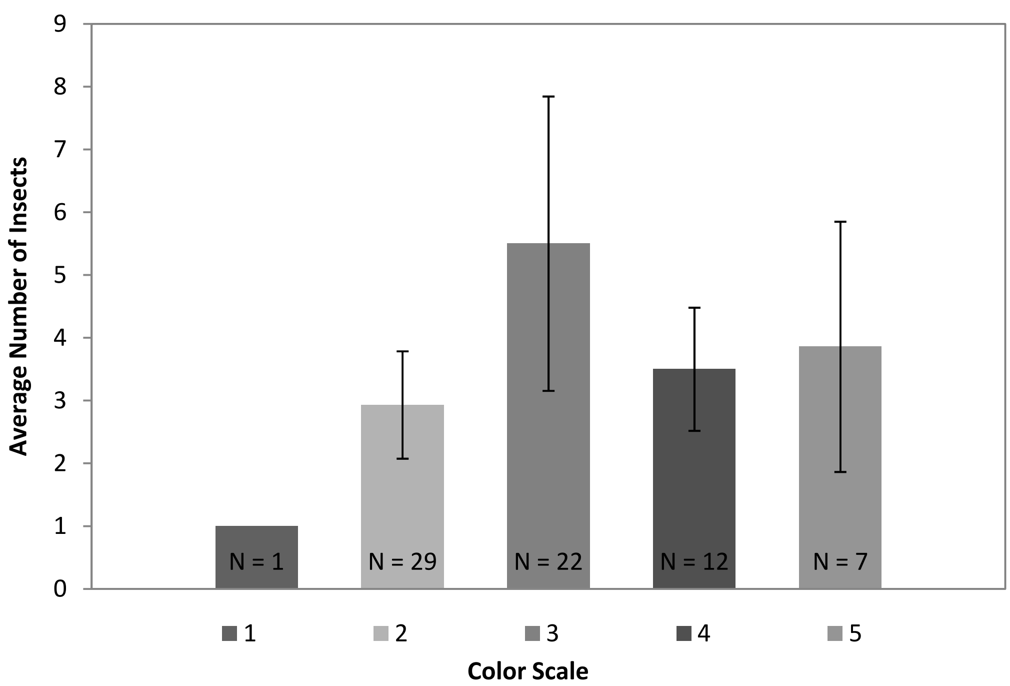


Figure 9. Average number of insects (± SE) in *Sarracenia Purpurea* pitchers divided into a color scale of 1-5 (1 = 0-20 % red, 2 = 21-40 % red, 3 = 41-60 % red, 4 = 61-80 % red, 5 = 81-100 % red).