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Source: Castanea, 81(2):83-90.
Published By: Southern Appalachian Botanical Society
DOI: http://dx.doi.org/10.2179/15-065
URL: http://www.bioone.org/doi/full/10.2179/15-065

CASTANEA 81(2): 83–90. JUNE

The Effects of Fire and Other Habitat Characteristics on Habitat Selection of *Exyra ridingsii* (Riley), the Riding's Pitcherplant Looper Moth

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ABSTRACT *Exyra ridingsii* is a host-specific moth that spends its entire immature life cycle in the *Sarracenia flava* L. pitcher plant. *Sarracenia flava* requires a habitat that undergoes frequent fires and has acidic moist soil. During this investigation we studied the degree to which *E. ridingsii* damaged *S. flava* under different environmental conditions. From summer 2012 to fall 2013, five sites in the Croatan National Forest, North Carolina, were surveyed four times each year. At each site, 7 to 20 quadrats were randomly selected for sampling. In each quadrat, pitchers were counted and measured for height and whether the pitchers were affected by herbivory; the fraction affected was calculated (herbivory per clump). Median herbivory per clump at the burned sites ranged from 86–100%. All other sites ranged from 50–75% with the exception of the unburned pocosin site, which was the lowest at 32%. Herbivory per clump was found to differ by site, but because sites varied in environmental characteristics other than burn status, other factors playing a role in habitat status cannot be ruled out. Tallest median trumpet heights were found at the unburned sites. During this study, *E. ridingsii* repopulated *S. flava* pitchers in the burned sites less than two months after fire, suggesting that they persist as a metapopulation.

Key words: *Exyra ridingsii*, habitat selection, Riding's Pitcherplant Looper moth, *Sarracenia flava*, yellow pitcher plant.

INTRODUCTION The yellow pitcher plant, *Sarracenia flava*, is a carnivorous species found in bogs and savannas throughout coastal Alabama, Georgia, North Carolina, and South Carolina (Evans 2005). The habitats occupied by the pitcher plant have frequent, low-intensity fires. In studies done on other closely related species, *Sarracenia alata* and *Sarracenia psittacina*, it was found that fires benefit plants because they reduce competition and release nutrients from soil (Barker and Williamson 1988, Brewer 1999). Like *S. alata* (Brewer 1999), the rhizome of *S. flava* can survive fires and sprout new pitchers, but this has not been studied in *S. flava*.

Many different arthropods can be found in pitcher plants; however, most of these species can find refuge and nutrition in other hosts. In contrast, *S. flava* is the only host to the noctuid moth, *Exyra ridingsii* (Folkerts and Folkerts 1996), and its larvae are commonly referred to as Riding's Pitcherplant Looper (Wagner et al. 2011). The entire life cycle of *E. ridingsii* occurs in *S. flava*, resulting in significant, distinctive herbivory by the larvae (Figure 1). This herbivory, however, rarely results in plant mortality (Atwater et al. 2006). The life cycle of the moth begins when the eggs are laid in the pitcher just below the opening (Jones 1921; Folkerts and Folkerts 1996). Larvae emerge and eat the inner layers of epidermal tissue, creating distinctive marks of herbivory (Figure 1). If larvae are found in the immature pitchers, they will close the pitcher by removing a ring of tissue

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Received June 30, 2015; Accepted May 5, 2016.
DOI: 10.2179/15-065

Figure 1. Herbivory on pitcher plants by *Exyra ridingsii*. This picture shows both the closing of the pitcher and the removal of epidermis. Photo taken summer 2012 in Croatan National Forest, North Carolina.

near the pitcher opening causing it to wilt inward (Folkerts and Folkerts 1996), a process known as girdling. In all other infested pitchers, the larvae create a secure feeding chamber by closing the pitcher with a silken web. Larvae continue to feed through five instars. Pupation also takes place in the pitcher, with the larva often cutting drainage and emergence holes in the pitcher. The adults are always seen in the pitchers with their heads up, feeding intermittently on the pitcher nectar before mating (Jones 1921). Due to the length of the growing season of their host plant in North Carolina, more than one generation per year is possible (Folkerts and Folkerts 1996). If necessary, pupae overwinter in the bottom of senesced pitchers after constructing a hibernaculum composed of frass, from which they emerge in the spring and reestablish populations in young pitchers (Jones 1921).

The wet, acidic soils that *S. flava* grows in are nutrient poor, which makes carnivory an important adaptation to gain elements important for growth, such as nitrogen (Adamec 2011). A symbiotic relationship between *S. flava* and *E. ridingsii* has evolved, with the latter dependent upon the former for survival with perhaps only limited effects at most on the survival of the plant despite the damage done by *E. ridingsii*.

In the longleaf pine forests of the North Carolina coastal plain where these pitcher plants are found, fires occur every one to five years and are usually caused by lightning strikes (Platt et al. 1988). After a fire has occurred, the clumps of pitcher plants that grow have more pitchers (Barker and Williamson 1988) and increased pitcher volume (Brewer 2005). In their study on *S. alata*, Barker and Williamson (1988) found that production in number of leaves in burned plots was three times that of the production in the unburned plots. In the absence of fire, *S. flava* plants are outcompeted by other plants found in the undergrowth (Brewer 1999, 2005) and are not as robust. Because *S. flava* is the only host for *E. ridingsii*, factors, such as fires, that affect plant populations may also have effects on moth populations (Tscharntke and Brandl 2004, Stephens et al. 2011). Further, because these moths persist in this fire-dependent environment, they must have a strategy to deal with periodic habitat loss. However, there has been no research on this topic. Stephen Hall, an invertebrate zoologist with North Carolina's Natural Heritage program, suggested that *Exyra fax*, a closely related moth species, may rely on a metapopulation strategy to repopulate burned areas (pers. comm., 2011).

For a metapopulation strategy to function, some individuals of the species would have to move from one habitat to another after a random extinction or fire has occurred. In order for a Lepidoptera population to become established in an unoccupied area, the area in question must have suitable habitat and be located near an established population to enable dispersal for colonization (Murphy et al. 1990, Folkerts and Folkerts 1996). Similar to *Exyra*, the males of the species *Neonympha mitchellii* are more likely to move than the females (Kuefler et al. 2008), but in order for a successful repopulation to occur after an extinction, the gravid females would also have to relocate. In their study of the moth, *Melitaea cinxia*, Hanski et al. (1994) did indeed find that females and males were equally likely to emigrate to a new patch of habitat. Atwater et al. (2006) suggested that even if adults exhibit low mobility, this would not prevent them from emigrating, which supports the metapopulation hypothesis.

The purpose of this study was to identify how quickly *E. ridingsii* inhabits *S. flava* after a burn and the extent of the infestation in the plant populations under different environmental conditions. It was hypothesized that the moths persist as a metapopulation with extinctions and repopulations at the burned sites. In addition, it was hypothesized that because *S. flava* is the only plant that *E. ridingsii* is known to inhabit, the population of the moth would increase after a burn due to the increased number of pitchers. This would be reflected with higher herbivory in the burned sites as compared to the unburned sites, as more *Exyra* would be found in the resulting healthier plants at the burned sites.

METHODS

Study Site

The Croatan National Forest is approximately 65,182 ha in size and is located in portions of Jones, Craven, and Carteret counties in the coastal plain of southeastern North Carolina (USDA Forest Service 2002). It encompasses three major ecosystems: longleaf pine forests, hardwood wetlands, and pocosins, which are coastal plain wetlands that are seasonally flooded with sandy, acidic soil, usually occurring in a depression on a hill (Richardson 1983, USDA Forest Service 2002).

Five 50 × 50 m plots were established in May 2012. Two plots, Millis 1 and Millis 2, were selected for the completeness of a controlled burn conducted between 12 March and 9 April 2012. This burn removed all litter and 70–80% of the understory vegetation (USDA Forest Service Report 2012). There were no visible pitchers in the plots after the fire. Three unburned sites (Catfish Lake Road, Millis 3, and White Oak Road) were also selected. All sites except Catfish Lake Road are considered longleaf pine savanna. Catfish Lake Road is considered a pocosin (USDA National Forest Service Report 2012). The U.S. Forest Service considers all of these sites areas of special interest due to their suitability as habitat for the red-cockaded woodpecker.

An origin was selected at each sampling plot, and its coordinates were recorded using the AllTrails application 2010 on an iPhone™ 4 with accuracy to 5 m. Seven to 20 randomly located 5 × 5 m sampling quadrats were installed in each sampling plot. The number of quadrats are as follows: Mills 3 had 7, Catfish Lake Road and Millis 1 had 10, Millis 2 had 11, and White Oak Road had 20. Differences in quadrats selected were due to flooding concerns and time constraints at the sites. Mapping was conducted using the ArcGIS online software (ESRI, Redlands, California) and Google maps to determine elevation and soil type.

Table 1. Soil saturation index (SSI) classification of the sites in the study. Each study site in the Croatan National Forest, North Carolina, was assigned an SSI value based on observed soil conditions.

SSI Class	Soil Condition
0	No water present, soil dry
1	Soil moist, no standing water
2	Standing water present, but pools of water not connected
3	Standing water present in connect pools up to 7 cm deep
4	Standing water present in pools from 7 cm to 24 cm deep
5	Standing water present in pools from 24 cm to 44 cm
6	Standing water present in depths greater than 44 cm

Sampling was conducted twice per season, two weeks apart at each site. At each site woody understory cover was estimated during the study using on-site observations and images using the following classifications: very open (cover <10%), open (cover 10–25%), some understory (cover >25% and <50%), overgrown (cover >50% but not impeding data collection), and very overgrown (cover >50% and dense enough to hamper data collection). A soil saturation index (SSI) was assigned to each site at each sampling. The SSI is a number ranging from zero to six representing the depth at which the soil was saturated and standing water was present (Table 1). The summed SSI from all sampling dates represented the overall soil moisture conditions during the study period.

The following measurements were recorded at each quadrat during each sampling: height of pitchers, herbivory class (healthy or showing herbivory), number of pitchers and pitcher density, number of clumps, and pitchers per clump. A clump was defined as all the pitchers appearing to sprout from the same rosette. We also calculated median pitcher height for each herbivory class. We calculated herbivory per clump (number of pitchers in a clump showing herbivory divided by total number of pitchers

Table 2. Summary of habitat characteristics, burn status, and coordinates of the origin for each site in the Croatan National Forest, North Carolina. This study was conducted over two years from May 2012 to October 2013.

Site	Origin Coordinates	Total Soil Saturation Index	Elevation (m)	Soil Type	Amount of Woody Understory	Burn Status
Catfish Lake Road	34.7393, −77.0300	34	11	Rains fine sandy loam	Very open	Unburned
Millis 1	34.7615, −76.7601	25	11	Mandarin sand	Open	Burned April 2012
Millis 2	34.7654, −76.9600	13	9	Mandarin sand	Some understory	Burned April 2012
White Oak Road	34.7393, −76.8822	8	9	Leon sand	Some understory	Unburned
Millis 3	34.7621, −76.9080	6	11	Leon sand	Very overgrown	Unburned

per clump) to allow comparisons of herbivory across time and sites. The sampling interval in late fall 2012 at Millis Road was delayed because of road closure, so data from these plots were collected starting 6 October.

Data from late summer 2013 were selected for statistical analyses because this date allowed *E. ridingsii* to exhibit maximum herbivory on *S. flava* before plant senescence. Because data did not follow a Gaussian distribution, nonparametric tests were conducted on median values using critical p values at $\alpha = 0.05$. A two-tailed Mann-Whitney U test was used to compare median height of pitcher between herbivory classes. Median values were used to minimize skewing of results by outliers. Kruskal-Wallis tests were performed to assess whether median height and herbivory per clump differed by site or burn status with Dunn's post hoc tests conducted to determine exactly which sites differed from each other. Burn status analyses were conducted by placing data into two groups, burned or unburned, rather than sites. Spearman's rank-order correlation tests were conducted to determine whether herbivory on pitchers was correlated to their density and whether herbivory per clump and height are correlated. Mean density values were used for this statistical test. Further Spearman's rank-order correlation tests were conducted to determine whether herbivory and height was correlated to height and amount of woody understory cover. The open source program R was used for all statistical testing (R Core Team 2013).

RESULTS The wettest site, Catfish Lake Road, was also the most open (Table 2) and had the tallest trumpets (Figure 2). Soil saturation index was found to be correlated to both height ($S = 678{,}300$, $p < 0.001$) and herbivory per clump values ($S = 17{,}006$, $p < 0.01$). This was the only site with the soil type of Rains fine sandy loam (Table 2). Millis 1 and Millis 2 were the sites that both had mid-SSI levels and the soil type Leon sand (Table 2). These two burned sites also had the shortest trumpets (Figure 2). Levels of woody understory cover were also found to correlate to herbivory per clump ($S = 5{,}164.5$, $p < 0.001$) and pitcher height ($S = 1{,}724{,}800$, $p < 0.001$).

Median pitcher heights were the tallest at the unburned sites, Catfish Lake Road, Millis 3 and White Oak Road (WOR), with the shortest pitchers found at the burned sites, Millis 1 and Millis 2 (Figure 2). These height differences were significant between Catfish Lake Road and all other sites (Catfish Lake Road–Millis 1, $Z = 7.26$, $p < 0.01$; Catfish Lake Road–Millis 2, $Z = 4.05$, $p < 0.01$; Catfish Lake Road–Millis 3, $Z = 2.86$, $p = 0.04$; Catfish Lake Road–WOR, $Z = 3.26$, $p = 0.001$). Tallest pitchers were always found at the pocosin site, Catfish Lake Road (Figure 2). Pitchers with herbivory were taller than healthy pitchers (Figure 2), but this difference was not significant ($W = 21{,}948$, $p = 0.56$).

The three unburned sites had the lowest herbivory per clump, which differed by site; specifically, Catfish Lake Road differed from both burned sites. The burned sites had the greatest herbivory per clump (Figure 3). There was no correlation between herbivory per clump and pitcher height ($S = 8{,}651.3$, $p = 0.51$) or density ($S = 26$, $p = 0.68$). However, sites with the tallest pitchers, Catfish Lake Road and White Oak Road, had the lowest herbivory per clump (Figure 3), while the sites with the shortest trumpets (Figure 2) had the highest herbivory per clump. The two burned sites, Millis 1 and Millis 2, differed significantly (Catfish Lake

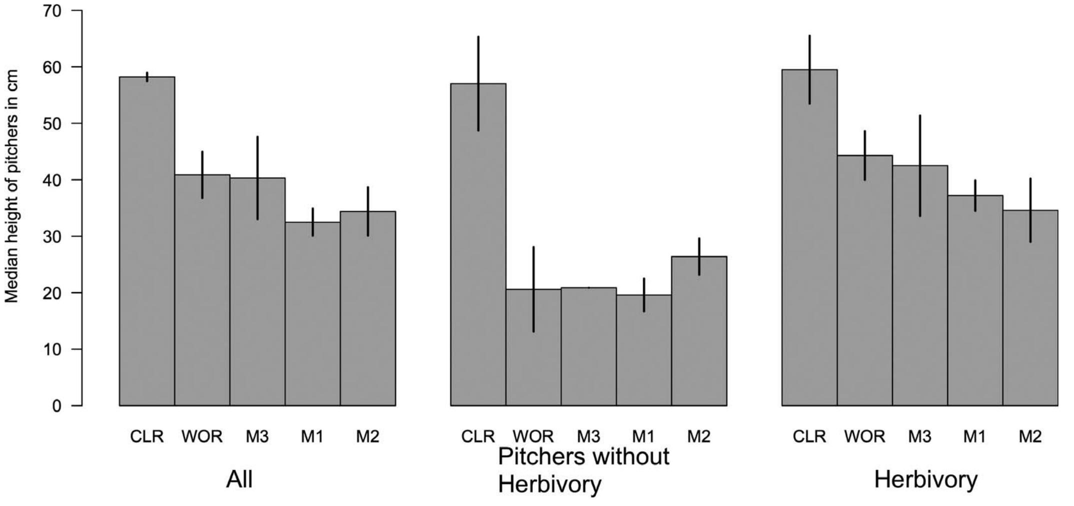

Figure 2. Median heights of pitchers by category with ±1 SE in cm at each of the sites in the Croatan National Forest, North Carolina, for the late summer 2013 sampling date. Sample sizes for all pitchers were Catfish Lake Road (CLR), n = 341; White Oak Road (WOR), n = 7; Millis 3 (M3), n = 5; Millis 1 (M1), n = 52; and Millis 2 (M2), n = 11. Sample sizes for pitchers without herbivory are CLR, n = 124; WOR, n = 4; M3, n = 4; M1, n = 40; M2, n = 8. Sample sizes for pitchers with herbivory are CLR, n = 217; WOR, n = 3; M3, n = 1; M1, n = 12; M2, n = 3.

Road–Millis 1, Z = –3.04, p = 0.002; Catfish Lake Road–Millis 2, Z = –2.53, p = 0.01) from the unburned site that was the farthest from them, Catfish Lake Road. There was no significant difference in herbivory per clump values between the other sites.

Moth immigration occurred into the burned sites, Millis 1 and Millis 2, by the late summer 2012 sampling date (Table 3). Moths were present in all sites at all sampling dates that *S. flava* was found after this date, with the exception of Millis 3, the driest site (Table 1,

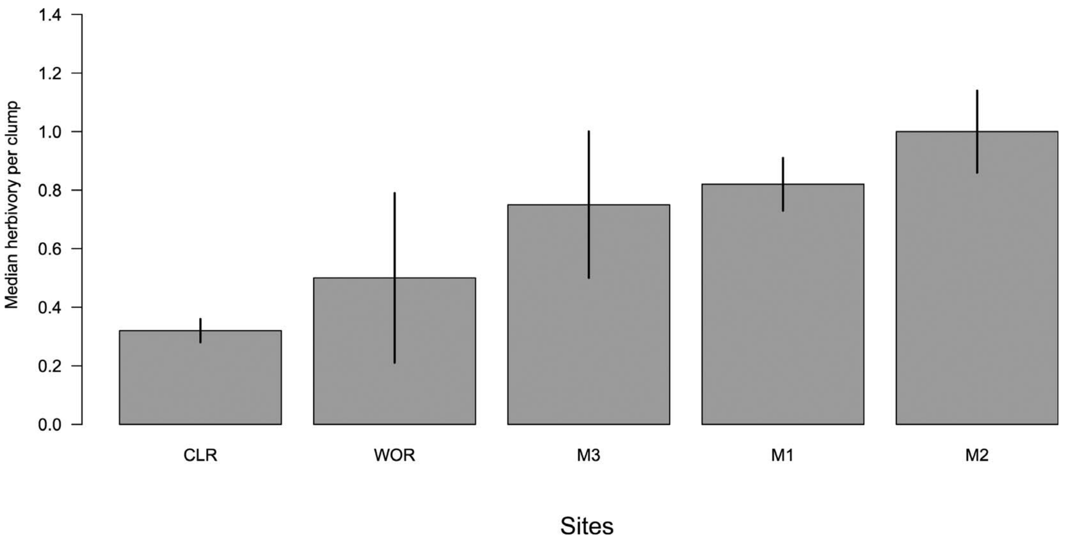

Figure 3. Median herbivory per clump values with ±1 SE for each of the sites in the Croatan National Forest, North Carolina, for the late summer 2013 sampling date. Sample sizes for each site were: Catfish Lake Road (CLR), n = 23; White Oak Road (WOR), n = 4; Millis 3 (M3), n = 2, Millis 1 (M1), n = 8; and Millis 2 (M2), n = 3.

Table 3. Median herbivory per clump values at each site for each sampling date of the study, conducted in the Croatan National Forest, North Carolina. A burn was conducted at the Millis 1 and Millis 2 sites before the study began.

Sampling Time	Millis 1	Millis 2	Millis 3	White Oak Road	Catfish Lake Road
Early summer 2012	0 (n = 18)	0 (n = 2)	0.3 (n = 2)	0.5 (n = 17)	0.4 (n = 35)
Late summer 2012	0.3 (n = 14)	0.1 (n = 6)	0.3 (n = 9)	0.9 (n = 8)	0.3 (n = 31)
Early fall 2012	0.5 (n = 11)	0.4 (n = 4)	0.6 (n = 6)	0.6 (n = 10)	0.9 (n = 11)
Late fall 2012	0.7 (n = 6)	0.5 (n = 2)	0.6 (n = 4)	0.7 (n = 11)	0.7 (n = 22)
Early summer 2013	0.1 (n = 17)	0.3 (n = 5)	0 (n = 4)	0.4 (n = 10)	0.2 (n = 36)
Late summer 2013	0.8 (n = 8)	1.0 (n = 3)	0.8 (n = 2)	0.5 (n = 4)	0.3 (n = 23)
Early fall 2013	0.8 (n = 8)	0.8 (n = 2)	1 (n = 3)	1 (n = 8)	0.7 (n = 17)
Late fall 2013	0.9 (n = 8)	Site flooded, no pitchers found	1 (n = 6)	1 (n = 5)	0.7 (n = 17)

Table 3). No moths were found on the last sampling date of the study at this site because it was completely flooded and no pitchers were visible (Table 3).

DISCUSSION During this study, it was hypothesized that *E. ridingsii* persists as a metapopulation. There was evidence to support this hypothesis, as moths returned to burned sites by the late summer 2012 sampling date. It was also hypothesized that because *E. ridingsii* only inhabits *S. flava*, there would be increases in the population of the moth in burned sites and this would be seen by increased levels of herbivory in *S. flava* as compared to unburned sites. This was expected because the *S. flava* in the burned areas would be healthier as a result of the fire and therefore would provide better habitat. The burned compared to unburned sites had higher herbivory per clump; specifically, Millis 1 and Millis 2 were higher compared to Catfish Lake Road. However, White Oak Road and Millis 3 were unburned sites that did not differ from the burned sites in herbivory. This may be explained by the fact that Catfish Lake Road was the only site that was a pocosin and was continuously flooded. Since both SSI and woody understory cover were correlated to herbivory per clump, these two characteristics may also play a role in habitat selection of *E. ridingsii*.

Moths were found in new pitchers on 3 June 2012, two months after the fire on 9 April that removed all existing pitchers, suggesting that they persist as a metapopulation. These moths may have immigrated from unburned *S. flava* populations in adjacent habitats. Adjacent suitable habitat is important because in their study on *Exyra semicrocea*, Stephens et al. (2011) were not able to find *E. semicrocea* in all study sites. They attribute this to habitat fragmentation and winter burns. In the study by Stephens et al. (2011), the larvae were overwintering so they were unable to move but in our study, the timing of the burn and the adjacent habitats allowed *E. ridingsii* to disperse into the newly grown pitchers. *Exyra semicrocea* has been observed moving from pitcher to pitcher at night after feeding (Stephens and Folkerts 2012). Even though *Exyra* is a genus that exhibits low mobility, this does not prevent them from migrating to new habitats (Atwater et al. 2006). Millis 1 and Millis 2 were sites that had just undergone fires and it was highly unlikely that any moths survived due to the completeness of the burn. Therefore, we expect that any moths found in the burned sites must have immigrated there from the nearby populations, supporting the metapopulation hypothesis. To gain further support for the metapopulation hypothesis, a future study should be done in which the moths are tagged to see if the unburned habitats were reservoirs for the burned sites (Haddad 1999).

The dispersal of moths is important, as dispersal levels can affect the community in which they inhabit. *Exyra ridingsii* is an important part of the community. *Exyra* remove flesh of the pitchers and without this tissue, the ability of the pitcher to capture prey and photosynthesize is reduced (Moon et al. 2008). During a study of the inquiline communities in *Sarracenia purpurea*, it was found that when the dispersal of predators increased, local and regional richness in this metacommunity also increased (Kneitel and Miller 2003). The movement of any species into and out of a community will play a role in the dynamics of that community (Kneitel and Miller 2003). As *E.*

ridingsii moves into and out of an area, their interaction with their community plays a vital role in the functioning and makeup of that community.

As the host plant relies on fires to maintain healthy populations, the habitat available to *Exyra* would not be as suitable at the unburned sites (with the lowest levels of herbivory) as at the burned sites. *Sarracenia flava* had the lowest amount of damage in the only site that was classified as a pocosin. This site was continuously flooded throughout the study and had the highest pitcher density. Herbivory per clump and pitcher density were not correlated. As a consequence we speculate that lower levels of herbivory in the pocosin may be because the eggs and pupae cannot survive in standing water.

Unexpectedly, the unburned sites had taller trumpets than the burned sites, since burned sites were expected to have healthier and, therefore, taller trumpets. This difference was only significant at the pocosin site (Catfish Lake Road), which had Rains fine sandy loam soil and was extremely wet compared to the other sites, with Mandarin and Leon sand at the burned sites. This high water table along with the high acidity (Goodwin 1987) found at Catfish Lake Road make ideal conditions for growing the tall pitchers we found. Soil saturation and woody understory were correlated to pitcher height, which may account for the taller pitchers, as *S. flava* need open, wet areas to grow.

This study was the first to examine the interactions between *S. flava* and *E. ridingsii* and we have evidence to support that *E. ridingsii* does indeed persist as a metapopulation as shown by its quick repopulation of the newly grown *S. flava*. We also found a correlation between moth herbivory and soil saturation, as well as moth herbivory and woody understory cover. The lowest infestations of *S. flava* are in the areas of highest saturation, suggesting that moths and pupae may need slightly different environmental conditions than *S. flava* to thrive.

ACKNOWLEDGMENTS We thank James Cherry of the Croatan National Forest for sharing his vast knowledge of the forest and its burn history. We would also like to thank Bo Sullivan for his assistance in finding suitable sites. Janet Ricci provided invaluable field support.

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