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Life History Aspects of *Exyra semicrocea* (Pitcher Plant Moth) (Lepidoptera: Noctuidae)

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Abstract - With as little as 3% of southeastern Coastal Plain pitcher plant bogs remaining, it is important to understand the life-history aspects of the endemic organisms that comprise this community. In this study, we elucidate aspects of the life history of *Exyra semicrocea* (Pitcher Plant Moth) by incorporating unpublished portions of a thesis from 1978–1979 with recent field and lab observations in 2010. We give morphological descriptions of both larvae and adults, as well as behavioral descriptions and mortality measures. In addition, population estimates of *E. semicrocea* were conducted from east Texas through North Carolina. Our surveys identified four isolated pitcher plant sites where *E. semicrocea* may have been extirpated. This information has important conservation implications for *E. semicrocea* and is applicable to other pitcher plant-endemic arthropod species.

Introduction

Pitcher plant bogs (wet pine savannahs and other habitats dominated by carnivorous plants) of the southeastern United States Coastal Plain are composed of a diverse and complex community found nowhere else in the world. This region contains 29 or more carnivorous plants, with the most conspicuous genus, *Sarracenia* (pitcher plants), containing eight or more of these species. Members of the genus are known to interact with a variety of organisms including bacteria (Kneitel and Miller 2002, Koopman and Carstens 2011), protozoa (Hegner 1926), rotifers (Bateman 1987, Bledzki and Ellison 2003, Kneitel and Miller 2003), and most notably, arthropods (Dahlem and Naczi 2006; Folkerts 1999; Goodnight 1940; Jones 1904, 1907, 1908). Pitcher plant interactions with arthropods as prey have garnered the most attention (Heard 1998, Wolfe 1981), but it is important to note that these plants promote a diverse array of interactions with various arthropod species. These include herbivory, pollination, parasitism, and predation of primary associates, as well as capture interruption (Folkerts 1999). Some of these interactions are so specific that many of these arthropods are found only in pitcher plant bogs.

Pitcher plant moths (*Exyra* spp.) are the most noticeable of the 17 or more species of endemic arthropods within pitcher plants (Folkerts 1999, Rymal and Folkerts 1982) and are among the more studied pitcher plant symbionts because of damage caused by larval stages on pitchers (Atwater et al. 2006, Moon et al. 2008). These noctuid moths, first described by Gueneé (1852) and later revised by Grote (1879), consist of three described species: *Exyra fax* (Grote), *E. ridingsii*

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(Riley), and *E. semicrocea* (Gueneé). *Exyra fax* is obligate in *Sarracenia purpurea* L. (Purple Pitcher Plant), *E. ridingsii* is obligate in *S. flava* L. (Yellow Pitcher Plant), and *E. semicrocea* is a generalist on all species of *Sarracenia*. Initial behavioral observations on these moths were reported by Jones (1921) and followed by various reports of range and life-history information (Benjamin 1922, Brower and Brower 1970, Folkerts and Folkerts 1996), but to date none have provided a detailed life history of any of the three species.

In this study, we focused on *E. semicrocea* by presenting information from the unpublished portions of the thesis of Rymal (1980) regarding (1) larva and adult morphology/development and (2) mortality factors across all life stages. Additional data are provided from recent observations made in 2010 on (3) adult behavior and (4) local abundance across the southeastern Coastal Plain. Together, with a thorough review of previously published information, we present a robust account of the biology of *E. semicrocea*.

Study Area

Life-history and behavior observations were conducted at Packer Bog (1978–79), Splinter Hill Bog (2010), and Weeks Bay National Estuarine Research Reserve Site (2010) in Baldwin County, AL (Fig. 1). Historically, Baldwin County possessed a large and continuous expanse of pitcher plant bog habitat, including the now pastured Packer Bog, the recently preserved Splinter Hill Bog, and, most likely, the area now preserved in Weeks Bay National Estuarine Research Reserve Site (Folkerts 1982). Within the past 100+ years, southern Alabama has undergone a severe reduction of natural habitat, with remaining bog habitat being managed by agencies such as Alabama Forever Wild, The Nature Conservancy, and the National Estuarine Research Reserve System. The bogs in this region are characterized by deep, poorly drained, and strongly acidic soils found in seep areas at the bases of slopes and along drainages. The soil is fine, sandy loam on 2 to 5 percent slopes and is very low in natural fertility, with low to medium content of organic matter. Runoff is slow, and areas that are not ditched are usually saturated with water from seepage areas (McBride and Burgess 1964). The prominent pitcher plant species found at each of the three sites was *Sarracenia leucophylla* Raf. (White Topped Pitcher Plant), with *S. purpurea* L. (Purple Pitcher Plant), *S. rubra* Walt. (Red Pitcher Plant), and *S. psittacina* Michx. (Parrot Pitcher Plant) also occurring at these locations. Surveys of *E. semicrocea* distribution were made in 2010 at eighteen sites across the southeastern Coastal Plain (Fig. 2).

Methods

Larval and adult morphology/development

Exyra semicrocea larvae were reared from fertilized eggs collected at Packer Bog in 1978 to 1) determine number of instars and 2) measure head capsule width of each larval stadium. Larvae (n = 25) were fed cut portions of White Topped Pitcher Plant leaves in glass petri dishes with moist filter paper at Auburn University. Daily observations were made to detect ecdysis, and widths of head capsule were measured on living larvae with an ocular micrometer. The width of the head capsule has traditionally been used to determine instar stage because head capsule growth is discrete and occurs with each ecdysis (Harman 1970, Hoxie and Wellso 1974, Watson and Johnson 1974). The resulting measurements were used in subsequent field observations to estimate the instar of the larvae. Duration of developmental stages (i.e., egg, larval instars, pupa) for *E. semicrocea* was monitored within tagged pitchers in the field during 1978–79 (n = 72). Adult lifespans were assessed in 2010 with pupae collected from Splinter Hill Bog, AL (n = 16), and reared in the lab at Auburn University. Sex of *E. semicrocea* adults was determined by detecting the presence of valvae covered by long scales in the male or the presence of a setose ovipositor in the female. All adults that emerged in the lab received a nectar substitute of simple sugar water, and information regarding duration as adult and number of eggs oviposited was recorded.

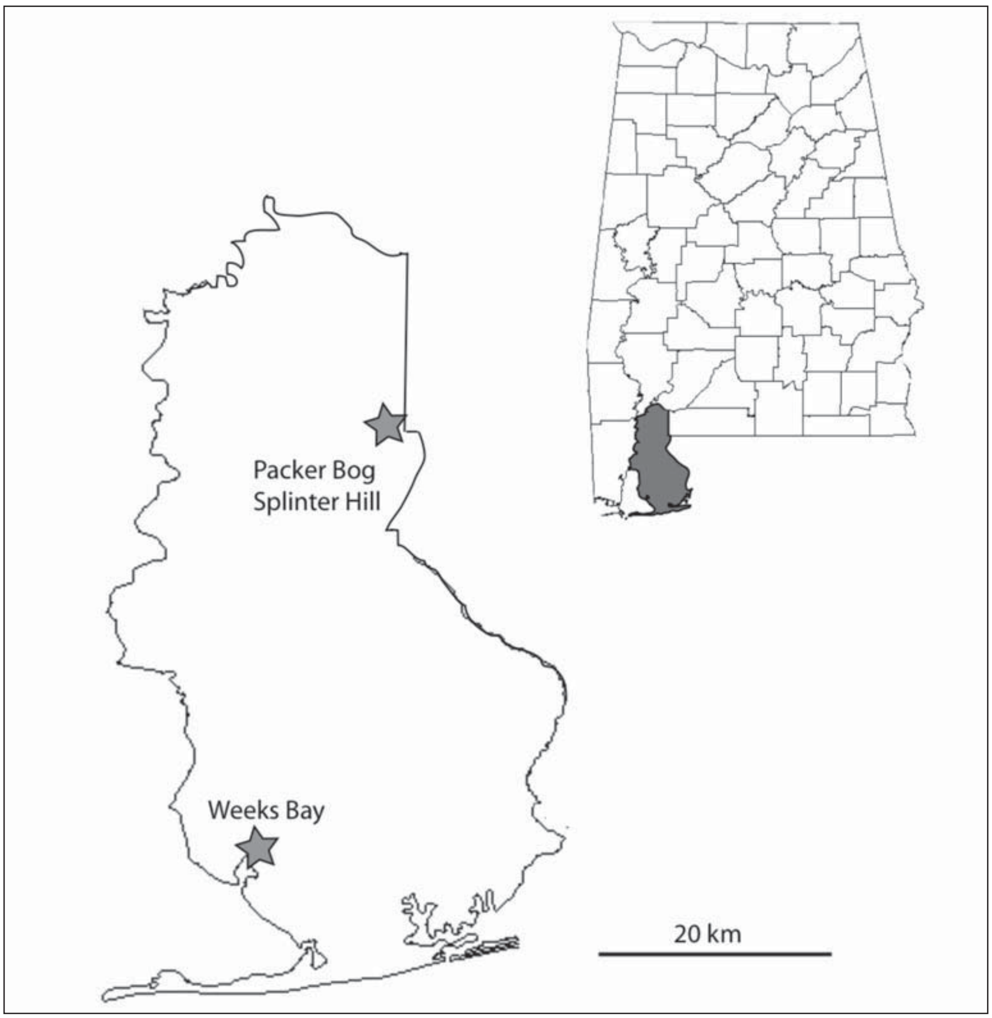

Figure 1. The three study sites located within Baldwin County, AL where behavioral observations of *Exyra semicrocea* were conducted. Due to their close proximity, Packer Bog and Splinter Hill Bog are represented by one star.

The original description of *E. semicrocea* was based on drawings and contained little information about larval morphology (Gueneé 1852). Crumb (1956) briefly described the larva based on a single preserved specimen. We have expanded this description and have provided an illustration of the fifth instar (Fig. 3). In addition, potential morphological adaptations in *E. semicrocea* adults, which apparently facilitate walking on downward pointing cellular projections of the pitcher plant leaf conductive zone, were evaluated using scanning electron microscopy (SEM) in 1978 and again in 2010. The ability to walk on the interior surfaces of *Sarracenia* spp. pitchers is apparently unique to Pitcher Plant Moths (Folkerts 1999). Therefore, pretarsal characteristics were compared between *E. semicrocea* and specimens of two non-pitcher plant-associated noctuids, *Helicoverpa zea* (Boddie) (Corn Earworm) and *Trichoplusia ni* (Hübner) (Cabbage Looper). The latter is a member of the Plusiinae, the same noctuid subfamily as *E. semicrocea*.

Adult behavioral observations

Observations of adult flight behavior were made twice a month from June through September 2010. Ten adults were marked during the day using a florescent dye powder (Magruder Color Company) and checked the following morning to assess emergence from leaves (n = 60). Additional adults were located and their respective pitchers flagged for nighttime observations of flight behavior. Each adult was sexed by making an incision into the wall of the pitcher and carefully using a hand lands to examine the lower abdomen. Leaves containing individuals were marked prior to dusk and monitored for movement throughout the night. Sex of individual, time of emergence, duration of flight, number of pitchers visited, duration inside pitchers, flight distance from original pitcher to final pitcher, and number of eggs oviposited were recorded. *T*-tests were conducted in the R v2.6.2 statistical software environment (R Development Core Team 2008) to test whether there were differences between sexes regarding time of emergence and lifespan.

Mortality measures

Percentage mortality in egg, larval, and pupal stages was calculated from tagged samples in Packer Bog in 1978–79 (n = 45, 287, 34 respectively), and periodic collections of larvae displaying signs of parasitism were brought back to the lab to rear and identify parasitoids. Dead larvae were also collected in order to ascertain mortality factors. Additional incidents of predation, parasitism, and fungal pathogens were recorded from incidental field observations made from 1978 through 2010. Finally, we collected a parasitized *E. semicrocea* larva and amplified the mitochondria (mtDNA) cytochrome *c* oxidase subunit gene (COI). The subsequent sequence was then compared to extant sequences in the NCBI database via BLAST (Altschul et al. 1990) in order to make an approximate identification of the parasitoid.

Population density

Surveys of local abundance and possible extirpation across the southeastern Coastal Plain were prompted by reports of declines in *E. semicrocea* abundance

(Folkerts and Folkerts 1996). During the summer of 2010, we sampled eighteen sites from eastern Texas through North Carolina in order to determine current status of *E. semicrocea* populations (Fig. 2). Exhaustive searches of every pitcher were conducted in small bogs to determine *Exyra* population size,

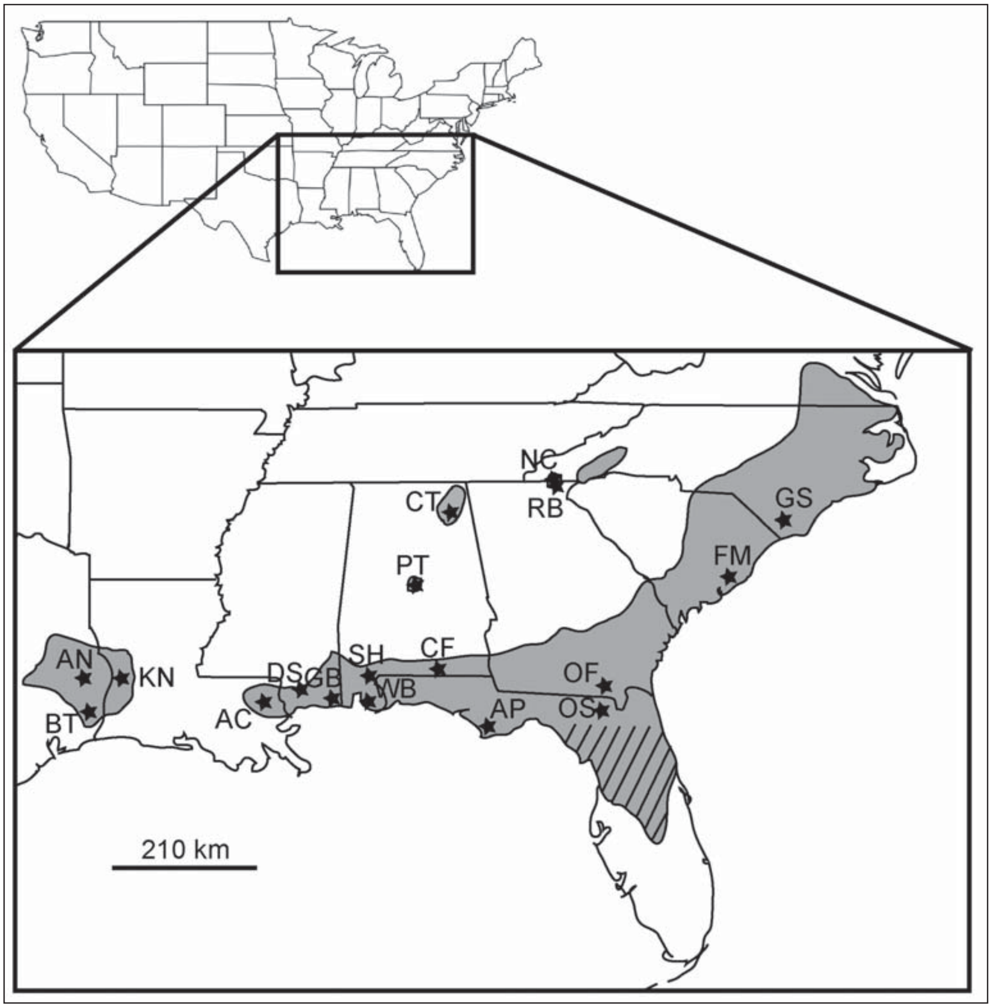

Figure 2. Shaded region represents historical range of *Exyra semicrocea* across the southeastern United States, with hash marks indicating historical range that may no longer contain bogs. The eighteen sites visited in 2010 are represented by stars. The three localities west of the Mississippi River are Angelina National Forest (AN), Big Thicket Nature Preserve (BT), and Kisatchie National Forest (KN). Populations sampled across the eastern portion of the range are Abita Creek (AC), DeSoto National Forest (DS), Grand Bay National Estuarine Research Reserve Site/National Wildlife Refuge (GB), Weeks Bay National Estuarine Research Reserve Site (WB), Splinter Hill Nature Preserve (SH), Conecuh National Forest (CF), Apalachicola National Estuarine Research Reserve Site/National Forest (AP), Osceola National Forest (OS), Okefenokee National Wildlife Preserve (OF), Francis Marion National Forest (FM), Green Swamp Nature Preserve (GS), Prattville Bog (PT), Centre Bog (CT), Reed Branch Nature Preserve (RB), and North Carolina Bog (NC).

while populations in larger bogs were estimated by extrapolating from counts in measured areas. Information regarding life stages and female/male ratio were recorded for each bog.

Results and Discussion

Development, morphology, and behavior

Egg. Descriptions of egg morphology have been presented previously (Folkerts and Folkerts 1996, Jones 1921), with both accounts noting the spherical shape and yellow hue. Eggs were an average diameter of 0.7 mm, with slightly undulating ridges radiating from a central point, where a micropylar area is evident. These ridges contain tiny pores that are most likely part of the egg respiratory mechanism (Wigglesworth 1972). Approximate time spent in the egg life stage was twelve days (Table 1).

An early report of *E. semicrocea* indicated that eggs are deposited singly due to the importance of having one larva per pitcher (Jones 1921). Observations by Folkerts and Folkerts (1996) indicated that number of eggs oviposited varied from one to several per pitcher. Results from 2010 support the latter: i.e., females oviposited anywhere from 1–3 eggs per pitcher. While previous observations could not ascertain whether eggs were oviposited by multiple females, recent observations were conducted through close monitoring of female nocturnal behavior. Therefore, we feel confident that a single female laid multiple eggs in a single pitcher in 2010.

Larva. Larval development of *E. semicrocea* spans five instars (determined from number of ecdyses in 1978–79), with head capsule size ranging between 0.32–1.78 mm (Table 2). Duration of stadia 1–3, stadia 3–4, and stadium 5 during summer months is roughly twelve, nine, and thirteen days, respectively (Table 1). Duration increases during colder temperatures when quiescence occurs. Overall,

Table 1. *Exyra semicrocea* average length of time in life stages.

Developmental stage	Avg. no. days	Range	S.D.
Egg	12	6–20	3.9
Larval stadia 1–3	12	7–15	3.2
Larval stadia 3–4	9	7–15	2.5
Larval stadium 5	13	8–21	5.2
Pupa	14	8–20	5.5
Adult	10	7–16	2.8

Table 2. Average measurements of *Exyra semicrocea* head capsule widths of instars one through five (n = 10).

Instar	Width of head capsule (mm)	SD
I	0.32	0.01
II	0.65	0.01
III	0.89	0.07
IV	1.32	0.10
V	1.78	0.21

the eruciform larva ranged from 4 mm in length during the first instar to 30 mm in length in the fifth instar, with segments having a bright red coloration and white intersegmental areas (Folkerts and Folkerts 1996, Rymal and Folkerts 1982). The head capsule of *E. semicrocea* is ivory with four incomplete and irregular black bars, and mandibles each possessing five teeth (Fig. 3a). An eversible gland is present on the ventromeson of the prothorax. Ventral prolegs (Fig. 3b) bear crochets in a biordinal mesoseries. There are approximately 26 crochets in the two series on A6, with the shorter series of crochets being bifid (Figs. 3c). The body is covered with microspinules, which occur in especially dense patches on the dorsum of A1–A4. The prespiracular group of setae on the prothorax is bisetose. D1, D2, and SD1 on the meso- and metathorax arise from chalazae. Paired lateral projections are found on abdominal segments one through four (Fig. 3b), with length decreasing rearward. These fleshy lateral projections, termed "lappets" (Jones 1921; Fig. 3b) are covered with microspinules and bear the SD1 seta at their apex. Lappets are absent in first instar larvae, are relatively narrow and elongate in instars two and three, and become enlarged in instars four and five.

The ability of *E. semicrocea* larvae to avoid entrapment in pitcher plants may be due in part to the function of the lappets (Folkerts 1999, Jones 1921). Larvae, when disturbed, will often curl their bodies and drop into the pitcher. The projecting lappets of these larvae prevent them from falling to the lowest, narrowest portion of the pitcher, which contains long, stiff, downward pointing hairs. Other important entrapment-avoiding mechanisms of the larva include a dragline of silk that is often used inside the pitcher to pull the larva up from the pitcher bottom and also for feeding on the inner leaf surface, which destroys the trapping function of the leaf.

Damage to the leaves by *E. semicrocea* has been well documented (Folkerts 1999, Folkerts and Folkerts 1996, Jones 1921, Moon et al. 2008, Rymal and

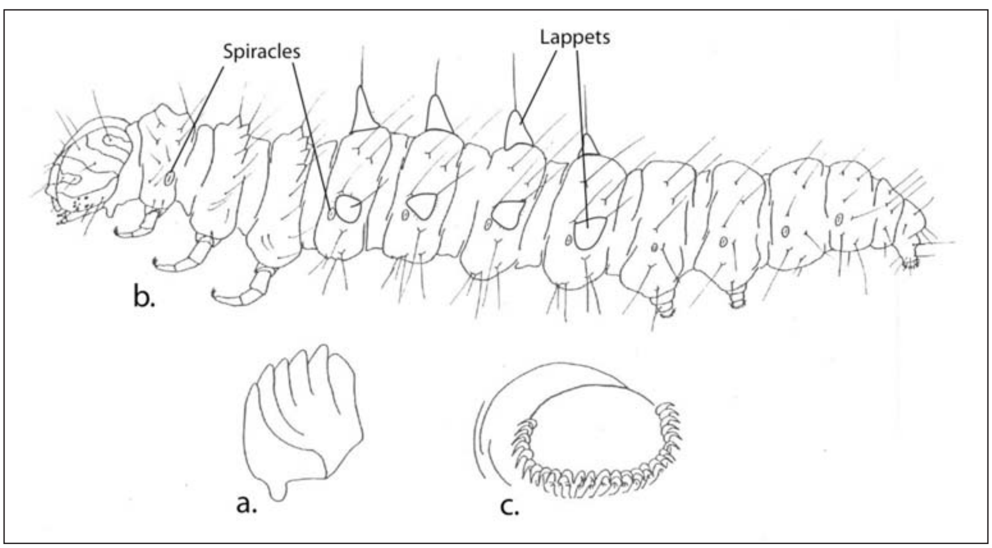

Figure 3. *Exyra semicrocea* larva: a) mesal view of the right mandible, b) lateral view of a fifth instar, and c) ventral view of the crochets of a proleg I.

Folkerts 1982). Typically, a first or second instar cuts a narrow feeding channel from within a young leaf, which encircles the pitcher and causes wilting above. The wilted portion of the leaf forms a hardened cap over the mouth of the pitcher and creates a protective feeding chamber (Folkerts 1999, Jones 1921). In contrast, feeding on mature pitcher plant leaves does not produce this wilting effect. Third, fourth, and fifth instar often produce a fine, silken web covering the opening of an inhabited pitcher (Folkerts 1999). A feeding chamber of this kind usually has a web ceiling, a floor of frass, which accumulates above the level of the prey mass, and walls formed by the membranous outer leaf surface, which remain after the inner leaf layers have been removed by feeding (Folkerts 1999). The web ceiling was observed to be an effective shelter against water intrusion during a gentle rain and also excluded potential spider predators (Jones 1921). It has been suggested that dispersal of larvae only occurs once the entire pitcher has been consumed because of inherent predation risk (Jones 1921), but Folkerts (1999) documented multiple migrations between pitchers during development. Usually movement between pitchers occurs shortly after the first instar hatches, during second or third instars, in the fifth instar, and finally before pupating. In most cases, the leaves are not completely consumed. Dispersal of first instar partly explains why more than one larva is rarely found in a leaf, even though several eggs may have been present. In a few instances, more than one larva has been found inhabiting a single pitcher, with webbing or a layer of frass separating them. This separation was also noticed in individuals reared in the lab in 2010.

Overwintering of *E. semicrocea* occurs as second, third, fourth, or fifth instars, with feeding ceasing in late November (Folkerts and Folkerts 1996). Various types of hibernaculae have been observed (Jones 1921). Small larvae are most often found near the bottom of the pitcher, having burrowed beneath the accumulation of prey. Large larvae are sometimes buried in frass or cling to dry pitcher walls, well above the level of frass and prey. Occasionally, chambers have web ceilings with particles of frass incorporated into the silk.

Pupa. The brown pupa is approximately 11 mm in length (Table 1). Before pupation, fifth instars disperse to pitchers that are usually undamaged and often cut a small hole (approximately 2 mm in diameter) in the lower portion of the pitcher tube (Folkerts 1999). Pupal chambers are located above these holes, which presumably function to drain excess rainwater. The cocoon varies from a few strands of supporting silk near the anterior end to a mesh of silken strands covering the entire pupa (Jones 1921). The simplest type of chamber contains a pupa, cephalic end up, suspended by silken strands attached to the interior wall of a pitcher with varying amounts of silk surrounding the pupa. A variant on this type of chamber is shielded above by a thin sheet of silk and bordered below by varying amounts of frass and silk (Jones 1921). The least common type of pupation chamber is found in pitchers with obvious feeding damage. In this case, the pupa is found beneath the level of frass in a silk-lined chamber only slightly larger than the pupa itself.

Adult. Adults are approximately 12.5 mm in length with wings folded. The forewing averages roughly 11 mm in length and has the most variable wing color patterns of the three *Exyra* spp. (Folkerts and Folkerts 1996). The common type has a black distal half of the forewing with a straw basal half and hind wings completely black or gray in color. Head and prothorax are black, with the remaining body, including the filiform antennae, being straw (Folkerts 1999, Jones 1921, Rymal and Folkerts 1982; Fig. 4). Two other forms of *E. semicrocea* with variations of the forewing pattern were described by Benjamin (1922) and Dyar (1904), with Benjamin's aberration validated by McDunnough (1938) when he listed it as a form. Moths have varying degrees of black mottling on the distal half of the forewing, which is combined with variation in shading of the hindwing. However, the variation does not show a geographic pattern, and specimens with all variations can be found at the same bog (Folkerts 1999).

Regarding avoidance of being trapped in the pitcher plant, *Exyra* adults have the apparently unique ability to walk on the interior of pitcher plant leaves (Folkerts 1999). While it has not been possible to examine the pretarsal position of a live adult within a pitcher, we can make assumptions about the potential functions of pretarsi in clinging to pitcher plant surfaces using scanning electron

Figure 4. *Exyra semicrocea* in copulation. The lower and lighter moth is the male.

micrographs (SEM) and comparative measurements. SEM revealed a difference in the shape of the pretarsal claws of *E. semicrocea* when compared to other noctuids, *H. zea* and *T. ni*. Unlike *H. zea* (Fig. 5a) and *T. ni* (not pictured), the metathoracic pretarsi of *E. semicrocea* (Fig. 5b) have bifid claw tips with arms of equal length, and claws projecting laterally, causing the empodium and aroliar pad to extend beyond the claws. This lateral projection of the claws also occurs in the mesothoracic (not pictured) and prothoracic pretarsi (Fig. 6); the claws of the prothoracic pretarsus are also bifid, but have thicker bases than in other legs. In *H. zea*, the arms of the claw's bifid tips are of unequal length, and the claw tips in the *T. ni* are not bifid. Although it is impossible to conclusively determine the function of these structures in *Exyra*, comparative measurements of claws and leaf projections lead us to believe they are used in placement of the pretarsus on the leaf surface. Cellular projections of the conductive zone in the White Topped Pitcher Plant are ≈10 μm wide at the base, tapering to a point, and ≈20 μm apart. Moth pretarsi have notches in bifid claw tips ≈10 μm wide and a width between tips of ≈20 μm (measurements were taken at multiple SEM angles not shown). Claw tips may be used in grasping leaf projections. Additional behaviors appear

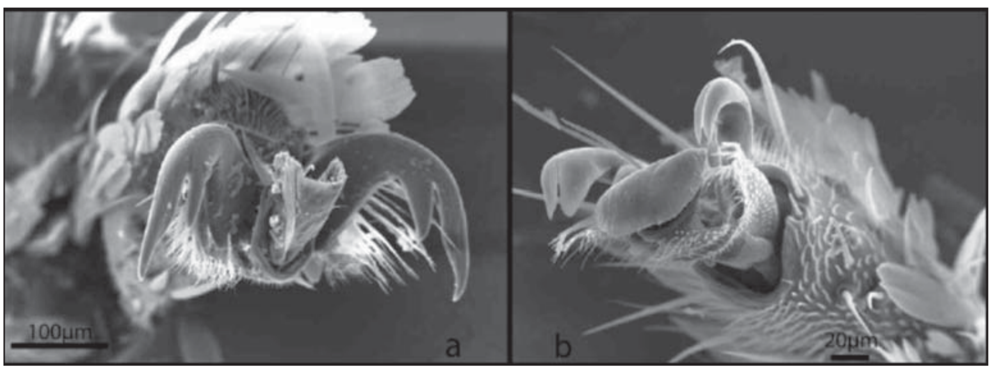

Figure 5. Scanning electron micrograph of the pretarsus of the adult metathoracic leg of a) *Helicoverpa zea* (magnification 500x) and b) *Exyra semicrocea* (1000x).

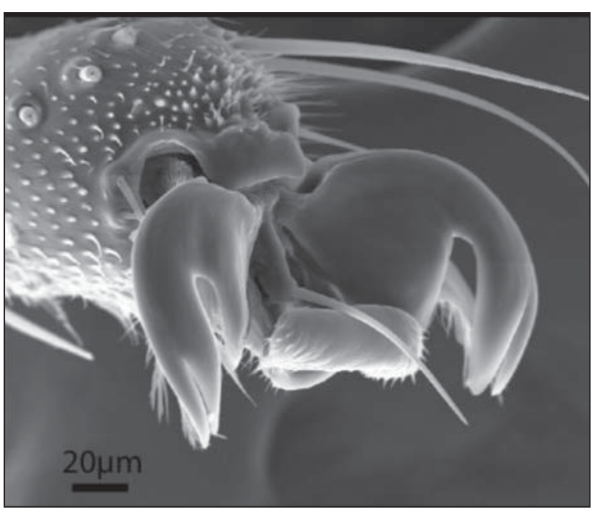

Figure 6. Scanning electron micrograph of the pretarsus of the adult prothoracic leg of *Exyra semicrocea* (1000x).

to be vital in trap avoidance, as *E. semicrocea* adults always perch in an upright position within pitchers, and even enter pitchers backward. Moreover, they copulate at a right angle (Fig. 4), which is in contrast to the end-to-end coupling typical in noctuids. This copulation position ensures neither moth is oriented with head downward in the pitcher. It is likely that a combination of morphological and behavioral traits allow *E. semicrocea* to avoid entrapment.

Additional behavioral observations of *E. semicrocea* suggest moths are mostly stationary and well below the orifice of the pitcher throughout the day. This is possibly an adaptation to avoid predation. Nighttime observations in 2010 revealed that moths begin to move prior to dusk, feeding on the extrafloral nectaries near the orifice of the pitcher before quickly retreating back to their sedentary position, thus confirming descriptions made by Jones (1921). This feeding behavior typically occurs one to six times before emergence from the pitcher for flight. Flight emergence occurred in all florescent dye-marked individuals (n = 60), as none were found in the original pitcher the following morning. Descriptions of nightly flight emergence made in 1980 indicated that *E. semicrocea* females emerge from pitchers shortly after dusk and fly to nearby pitchers. Males emerge soon after and fly in search of females within pitchers. Observations made in 2010 supported these inferences and revealed that female moths tend to leave ≈24 minutes after sunset (range of 9–55 min). Females usually fly to nearby pitcher plants and rarely venture high above the bog. Female flight time was from 2–30 minutes ($\bar{x}$ = 13), with an average distance of 16.84 m (n = 12). During this time, females often visited multiple pitchers ($\bar{x}$ = 4), typically staying less than 1 minute (although three females stayed in visited pitchers for over 30 minutes). Three out of seven females that were observed in pitchers with males during the day oviposited 1–3 eggs in those pitchers. Oviposition by females in the lab revealed a range from 0–93 ($\bar{x}$ = 41, n = 5) eggs. These numbers suggest that females have the ability to lay numerous eggs per pitcher over their average ten-day lifespan as adults (no difference in male and female lifespan t = -0.9976, df = 14, P = 0.3354; Table 1).

In contrast to females, males exhibited a more erratic flight pattern and were therefore harder to observe. The average male emergence time was 3 hours and 32 minutes after sunset, with the earliest emergence being 1 hour and 5 minutes after sunset. This emergence time is significantly different from females (t = -8.4349, df =15.477, P < 0.001). Measures of male flight time and distance were unattainable due to the quickness of males and their tendency to fly several meters above the bog. Males seen in the field appear to be lighter in color than females due to a loss of wing scales that likely occurs during flight (Fig. 4). This observation, when compared to sedentary captive males that retain their dark coloration in the lab, indicates that males potentially engage in more flight than females, as is necessary in the search for receptive females. This greater tendency for flight by males is further supported by a light trap study of *E. fax*, in which mainly males were caught, indicating that males of that species also fly more frequently (Brower and Brower 1970).

Mortality measures

Mortality in the egg stage was recorded at 56% in 1978–79 (Table 3). This rate of mortality is assumed to be the combined results of infertility, predation, fungal pathogens, and parasitism. Although egg predation was never witnessed, several small spiders capable of preying upon eggs in pitchers were observed. Eggs appearing to have been parasitized were distinguished by a silvery black color and tiny exit hole in the eggshell. The egg parasitoid was never captured and identified, but is believed to be a hymenopteran. This hypothesis is supported by previous observations of *E. semicrocea* egg parasitism by a presumed species of Chalicidoidea in a bog in North Carolina (Jones 1921).

Larval mortality is difficult to ascertain, as disappearance of larvae from tagged pitchers was often due to dispersal to nearby pitchers. Therefore, a disappearance rate was calculated at 60% and observed mortality at 15% (Table 3). Predation of dispersing larvae was observed on multiple occasions between 1978 and 2010 by spiders (i.e., *Peucetia viridans* (Hentz) [Green Lynx Spider], *Strotarchus piscatoria* (Hentz) [Bent-leaf Spider], and *Phidippus audax* (Hentz) [Common Jumping Spider]) and *Solenopsis invicta* Buren (Formicidae; Red Imported Fire Ant). Fire ants and *S. piscatoria* have also been seen preying on *E. semicrocea* larvae within pitchers. Additional mortality of *E. semicrocea* larvae within pitchers was due to an unidentified tachinid parasitoid, a braconid parasitoid, and the fungal pathogen *Nomuraea rileyi* (Farlow) (Moniliaceae). The fungal pathogen attacks larvae of all instars and was most commonly seen in late fall. The tachinid parasitoid emerges as a larva from the fifth instar and was most commonly seen during the overwintering period. The braconid parasitoid was collected as a pupa from a third instar in 1978. In addition to predation and parasitism, larvae have been witnessed to drown in pitchers after severe storms.

The pupal stage incurred 29% mortality, primarily the result of spider predation (Table 3). For example, Bent-leaf Spiders preyed upon 50% of the tagged pupae during a one-week period in 1978. In addition, a hymenopteran parasitoid mitochondrial cytochrome oxidase subunit I (COI) sequence (97% match with *Diadegma semiclausum* (Hellén) [Ichneumonidae] within the NCBI database) was discovered in one pupal sample from a study in 2010 (data not shown).

Table 3. Mortality factors for *Exyra semicrocea* in *Sarracenia leucophylla* in Baldwin County, AL.

Lifestage	*n*	Mortality	Mortality factors	Noted predators and parasites
Egg	45	56%	Infertility, fungal pathogen, parasitism, predation	Unknown
Larval	287	75%*	Dispersal, fungal pathogens, predation	Bent-leaf Spider, Green Lynx Spider, Jumping Spiders, Red Imported Fire Ants, Fungus, tachinid (unidentified), braconid (unidentified)
Pupa	34	29%	Parasitism, predation	Bent-leaf Spider
Adult	N/A	N/A	Dispersal, predation	Lycosids, Odonates, Green Lynx Spider, Chiroptera

*60% missing, 15% observed mortality.

Percent mortality in the adult stage was not estimated, as adults could not be tracked in the field. However, a variety of predation events have been witnessed in incidental field observations. *Exyra semicrocea* does not fly during the daytime unless disturbed from the pitcher. When this occurs, dragonflies have been observed to be diurnal predators. Nocturnal predators are generally bats and spiders. For example, predation of a female moth in flight by a wolf spider was observed during the 2010 observations. It has also been noted on several occasions that dead adult *Exyra semicrocea* were present and still in the upright position within the pitcher, with no apparent cause of death.

Population density

Numbers, life stages, and sex ratios varied substantially across all sampled sites (Table 4), which is typical for a multivoltine insect. Individuals were not found at four localities (i.e., CT, PT, RB, NC; see Fig. 2 for abbreviations), although *E. semicrocea* had been previously recorded at those sites (D.R. Folkerts, pers. observ.; M. Hodges, The Nature Conservancy, Atlanta, GA, pers. comm.). These sites are home to small, isolated pitcher plant bogs composed of one or two federally endangered pitcher plants (i.e., *S. oreophila* (Kearney) Wherry [Green Pitcher Plant], *S. rubra* ssp. *alabamensis* (F.W. & R.B. Case) Schnell [Alabama Pitcher Plant]; USDA NRCS 2009). An exhaustive search of all pitchers at AC, AN, OS, OF, FM, and GS bogs revealed low abundance, potentially due to limited, patchy habitat. For example, bog habitat in OF, OS, and FM was mostly found along roadsides, with patches of interior bog at OF and FM; AN has recently undergone bog restoration. On the other hand,

Table 4. Numbers of *E. semicrocea* at eighteen sites (see Fig. 2 for site localities and corresponding names) surveyed during May–June 2010.

Site	*n*	Area surveyed (ha)	Density (#/per ha)	# larvae	# pupae	# adults	F:M ratio
AN*	3	0.25	12	3	0	0	n/a
BT	30	0.15	300	13	3	14	3:4
KN*	32	0.25	128	0	0	32	1:1
AC*	30	3.00	9	21	0	9	2:7
DS	30	2.00	16	28	0	2	1:1
GB	30	2.75	11	0	0	30	1:2
WB	54	1.21	44	15	1	38	11:8
SH	27	1.11	24	9	1	17	7:10
CF	29	0.74	39	28	0	1	1:0
CT*	0	0.10	0	0	0	0	n/a
PT*	0	0.08	0	0	0	0	n/a
AP	30	0.52	60	0	0	30	1:2
OS*	5	0.04	125	5	0	0	n/a
OF*	22	0.36	61	19	3	0	n/a
RB*	0	0.18	0	0	0	0	n/a
FM*	18	0.16	113	11	5	2	1:1
GS*	17	2.75	6	17	0	0	n/a
NC*	0	0.28	0	0	0	0	n/a

*Indicates sites that were exhaustively searched.

other bog habitats, such as AC, were large but had not been burned recently, and therefore, pitcher plants were less dense. The low population numbers of *E. semicrocea* at GS and FM may be influenced by competition with a sister species, *E. ridingsii*. *Exyra ridingsii* only inhabits the Yellow Pitcher Plant, which extends from Alabama into North Carolina. The abundance of *E. ridingsii* appears to shift with increase in latitude, from being rare to absent in the southernmost portion of Yellow Pitcher Plant range to replacing *E. semicrocea* in leaves of Yellow Pitcher Plant in the northern portion of the range (J.D. Stephens, pers. observ.). While this observation may not be the case year-round, this potentially competitive interaction (exclusion) of *E. semicrocea* from Yellow Pitcher Plant was also noted in another population in South Carolina in the early 1900s (Jones 1921). The abundance of *E. ridingsii* throughout its range, as well as effects on *E. semicrocea*, has not been studied.

Conservation implications

The lack of *E. semicrocea* at four sites surveyed, low abundance at other sites, and loss of bog habitat (e.g., Packer Bog and the peninsula of Florida) is of serious concern, especially with estimates predicting that perhaps 3% of original bog habitat remains due to fire restriction, urbanization, forestry, and agriculture (Folkerts 1982, Folkerts and Folkerts 1993). This decline in bog habitat has resulted in fragmentation of once continuous bog habitat (Folkerts 1982). Current management practices to preserve these fragments often involve prescribed burns conducted during the dormant season (i.e., winter burns). While these fires are beneficial to the plants, they may have negative effects on members of the arthropod community that are not adapted to winter burns. For example, *E. semicrocea* populations overwinter as larvae, are unable to disperse, and are likely to be severely damaged by winter burns (death of larvae in even a light burn has been observed). When prescribed burns involve the entire bog area, as is often the case in small and isolated fragments, no insects survive to repopulate those areas after the burn. Therefore, more research to address winter fire effects on the pitcher plant community is warranted, especially given the great diversity of endemics and associates inhabiting pitcher plant bogs. Maintaining and restoring pitcher plant bogs in the southeast is vital to preserving these communities for future generations.

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