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# Ecological Interactions Between Spiders and the Purple Pitcher Plant, *Sarracenia purpurea*

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**ECOLOGICAL INTERACTIONS BETWEEN SPIDERS AND THE PURPLE PITCHER PLANT, *SARRACENIA PURPUREA***

by

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**ABSTRACT**

ECOLOGICAL INTERACTIONS BETWEEN SPIDERS AND THE PURPLE PITCHER PLANT, *SARRACENIA PURPUREA*

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Spiders and harvestmen are commonly captured by or reside upon the carnivorous purple pitcher plant, *Sarracenia purpurea*. Although spiders and harvestmen are often known to be prey of *S. purpurea*, other ecological interactions between these arthropods and the plant are poorly understood. Studies were undertaken at three pitcher plant populations, two in Virginia and one in North Carolina, to assess the ecological relationships between spiders and harvestmen and *S. purpurea*. Multiple plots containing pitcher plants (treatment) and plots lacking pitcher plants (control) were created at these locations. Spiders and harvestmen were collected through five different techniques. Spatial, temporal, and interspecific variation in spider diversity and density among these techniques was calculated. To assess the attractive and/or retentive ability of the morphological features of *S. purpurea*, a field experiment was carried out whereby pitcher plant types and models were placed in a large area and their capture abilities were compared. Sticky traps at various proximities from the plant were used to test the plant's influence on local insect density. The propensity of spiders and harvestmen to consume *S. purpurea* nectar was also examined, and the species of spiders that commonly oviposit in the pitchers were recorded. Finally, stable isotope signatures were used to determine if spider residents contribute nutrients to the plant. Significant correlations were found between the density and diversity of spiders captured by *S. purpurea* and those found in the environment. There was no difference in spider diversity or density between control and treatment plots. Pigment-lacking, peristome nectar-lacking, and control pitchers did not differ in arthropod capture, but models captured less prey. Furthermore, newer pitchers captured more prey than older pitchers. These data indicate that

attraction and/or retention of spiders by *S. purpurea* is similar to attraction and/or retention of insects. Spiders and harvestmen readily consumed *S. purpurea* nectar and often used the plant for oviposition. Spider residents of the genus *Agelenopsis* contributed nitrogen to the pitchers. Finally, there was no difference in insect density between control and treatment sticky traps, suggesting that *S. purpurea* does not influence nearby insect density.

For my amazing parents and my wonderful wife.

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# CHAPTER I

## INTRODUCTION

The purple pitcher plant, *Sarracenia purpurea*, is a carnivorous plant that traps and digests organisms through the use of pitcher-shaped leaves filled with rainwater and enzymatic secretions (Lloyd 1942, Schnell 2002). The plant is perennial with decumbent leaves, each with an autotrophic keel attached to a pitcher that is both autotrophic and heterotrophic. The pitcher absorbs nutrients from insects and also has photosynthetic pigments (Schnell 2002). The pitcher consists of a hood with red pigmented venation (except for the unpigmented forms), a nectar roll on the edge of the pitcher opening, and a long hollow stalk – wide near the top along the hood and narrowing towards the base – that forms the pitcher (Lloyd 1942, Schnell 2002).

*Sarracenia purpurea* is considered "carnivorous" as opposed to "insectivorous" due to its ability to consume not only insects, but spiders, mites, slugs, frogs, and even lizards (Lloyd 1942, Judd 1959, Wray and Brimley 1943, Purves et al. 2004). Each pitcher whorl consists of an average of six (Harvey and Miller 1996) to eight (Fish and Hall 1978) prey-trapping pitchers and/or mainly autotrophic "phyllodia" (Ellison and Gotelli 2002). While not true phyllodia, *S. purpurea* "phyllodia" are pitchers with a greatly reduced pitcher trap and an expanded autotrophic keel (Ellison and Gotelli 2002).

The pitcher morphology was described as having four zones by Hooker (1875) and a fifth was later added by Lloyd (1942). Zone 1 consists of the hood of the pitcher, possessing downward facing hairs and pigmented lures that lead into the pitcher trap (Hooker 1875, Lloyd 1942). Zone 1 also contains numerous nectar glands, as observed by scanning electron microscope (SEM) (Adams and Smith 1977). These nectar glands are located on the entirety of the exterior of the pitcher (Russel 1919, Juniper et al. 1989) but are most concentrated on the lip

Model article: Griffen, B. D., and D. G. Delaney. 2007. Species invasion shifts the importance of predator dependence. Ecology 88:3012-3021.

(peristome) in Zone 2 (Adams and Smith 1977, Joel 1986, Juniper et al. 1989, Cipollini et al. 1994). Zone 2 consists of the area surrounding the pitcher opening, internal to the nectar roll and down inside the pitcher to approximately 1 cm (Lloyd 1942). This zone has a smooth surface, slight venation, and also holds nectar glands (Adams and Smith 1977). The smooth surface surrounding the entrance to the pitcher causes organisms to fall into the pitchers. Once they are in the liquid, the slippery smooth surface and downward-facing hairs of the inner pitcher prevent escape (Anonymous 1885, James 1885, Lloyd 1942). Zone 3, the largest zone, is smooth and glossy (Lloyd 1942). Even though several authors have reported nectar glands on the inner surface of zone 3 (see Lloyd 1942), SEM examination reveals these "glands" to be fenestrations similar to stomata (Adams and Smith 1977). Lower down into the pitcher is Zone 4, an area that has downward pointing hairs but lacks glands, stomata, and cuticle (Lloyd 1942). Zone 4 does most of the absorption of nutrients (Adams and Smith 1977). Digestion occurs through enzymatic secretions from bacteria (Prankevicious and Cameron 1989, 1991) and enzyme-secreting glands located on the inner pitcher surface (Lambert 1902, Robinson 1908, Hepburn et al. 1920, Gallie and Chang 1997). Finally, below Zone 4 is Lloyd's (1942) Zone 5. Zone 5 holds some hairs yet has a mostly smooth interior surface and may also be involved in absorption (Lloyd 1942).

*Sarracenia purpurea* was split into two subspecies by Wherry (1933) in the early 1930s and the separation has generally been accepted (Schnell 2002). The two subspecies are *Sarracenia purpurea purpurea* (the northern variety) and *Sarracenia purpurea venosa* (the southern variety, located in Virginia and North Carolina) (Lloyd 1942, Schnell 2002). The northern variety of *S. purpurea* reaches its southernmost limit in mid-Maryland. The southern variety of *S. purpurea* reaches its northern limit in Maryland, causing a slight overlap and potential for interbreeding between subspecies (Schnell 2002). There is only a slight morphological difference between the subspecies; the *purpurea* subspecies has a more elongated pitcher and a thinner hood than the *venosa* subspecies (Schnell 2002).

One form of *S. purpurea purpurea* is *S. purpurea purpurea* f. *heterophylla*. This form lacks the ability to produce the reddish pigment anthocyanin, and thus has a green color (Schnell 2002). The plant occurs in Massachusetts, Connecticut, New York, Pennsylvania, Michigan, Minnesota, Ontario, and Newfoundland, and has been found thriving adjacent to its pigmented relatives (Sheridan 1997, Schnell 2002). Additional studies comparing the capture rates of the two plants are warranted (Sheridan 1997).

The nectar of *S. purpurea* has been shown to be the main pitcher feature that aids in prey capture (Jones 1923, Joel 1986; Dress et al. 1997; Deppe et al. 2000, Bennett and Ellison 2009). Only the lip of *S. purpurea* contains measurable amounts of nectar (Cipollini et al. 1994, Deppe et al. 2000). The nectar contains carbohydrates, simple sugars (Cipollini et al. 1994, Deppe et al. 2000), amino acids (Dress et al. 1997), but not coniine, the paralyzing agent that is present in the nectar of the yellow pitcher plant, *Sarracenia flava* (Lambert 1902, Mody 1976, Schnell 2002). Environmental conditions have little effect on the concentration of nectar (Deppe et al. 2000), which has been shown to be greater than 50% sucrose (Ne'eman et al. 2006).

The pigment in *S. purpurea* flowers and pitchers is composed of anthocyanins, specifically cyanidin and delphinidin (Sheridan and Griesbach 2001). The distribution of pigment within the leaves varies from almost absence to a shade of red throughout the leaf (Schnell 2002). Nectar droplets on the leaves of many carnivorous plants, including *S. flava*, absorb ultraviolet light to produce a pattern that highly contrasts with the surrounding leaf (Joel et al. 1985, Globner 1992). However, studies of the ultraviolet patterns on *S. purpurea* have not been conducted.

Carnivorous plants have been assumed to attract prey through a combination of morphological features, including nectar lures (Darwin 1875, Adams and Smith 1977; Dress et al. 1997; Deppe et al. 2000), pigmentation (Edwards 1876, Fish and Hall 1978), ultraviolet (UV) absorption (Joel et al. 1985, Juniper et al. 1989), and pigment-deficient spots on the back of the pitchers called fenestrations (although lacking in *S. purpurea*) (Pietropaolo and Pietropaolo

1986). In addition, prey may randomly encounter and fall victim to carnivorous plants (Hutchens and Luken 2009). Insects are captured more by newer pitchers (Fish and Hall 1978) with large amounts of red pigment (Shaefer and Ruxton 2008), small amounts of water (Newell and Nastase 1998), high amounts of nectar (Cresswell 1991), and a larger size (Cresswell 1993). However, studies (Sheridan et al. 2000) and observations (Schnell 2002) with pigment-lacking varieties of *Sarracenia* have shown that this form seems just as efficient at prey capture as its pigmented relatives, casting the role of pigment in prey capture into doubt. Clearly, the difficulty in teasing out each attractant creates limited quantitative evidence to support these hypotheses. Temporal, spatial, and density-dependent variation in any given environment have been proposed to play a large part in the trapping efficacy of carnivorous plants (Zamora 1995, Schnell 2002). Structural and temporal factors may also determine the attractiveness of each pitcher at luring prey. Furthermore, prey visitation to pitchers does not correlate with pitcher features that allow for high capture rates. Newell and Nastase (1998) concluded that prey visitation does not correlate with pitcher age or size. Moreover, potential prey visit carnivorous plant leaves and surrounding vegetation at equal frequencies (Williams 1976, Zamora 1995).

*Sarracenia purpurea* has been the center of numerous studies that have examined the contents of its pitchers. Although *S. purpurea* occasionally captures larger organisms such as mice, frogs (Lloyd 1942), salamanders (personal observation), and mollusks (Heard 1998), the majority of prey are arthropods (Wray and Brimley 1943, Judd 1959, Cresswell 1991, Heard 1998). Of the arthropods captured by *S. purpurea*, most are either insects (80%: Heard 1998 – 99%: Cresswell 1991) or spiders (1%: Cresswell 1991 – 3% Heard 1998). Yet, Heard (1998) also found large numbers of mollusks (10%) and mites (4%) captured by *S. purpurea*. Out of all four studies, there were only two harvestmen (Opiliones) captured (Wray and Brimley 1943).

Within the liquid of *S. purpurea* pitchers lives an aquatic phytotelmatous community of invertebrates. Macro-invertebrates include the larvae and pupae of the pitcher plant mosquitoes, *Wyeomyia smithii* (Culicidae) and *Wyeomyia haynei*, the pitcher plant midge, *Metriocnemus*

*knabi* (Chironomidae), and two species of flesh-fly in the family Sarcophagidae: *Sarcophaga sarraceniae* and *Fletcherimyia fletcheri* (Dahlem and Naczi 2006). Only one species of pitcher plant mosquito lives within a pitcher plant population at a time and the two species are geographically separated at almost the same location that the two subspecies of *S. pupurea* are separated – near Maryland's latitude (Schnell 2002). Micro-invertebrate phytotelmata include rotifers, protozoa, and bacteria (Cochran-Stafira and Ende 1998, Mouquet et al. 2008). On rare occasions other organisms also inhabit the water inside *S. purpurea* leaves, including larvae of the dobsonfly, *Chauliodes pectinicornis* (Hamilton et al. 1996), alderfly, *Sialis joppa* (Mather 1981, Pittman et al. 1996), Asian tiger mosquito, *Aedes albopictus* (Milne et al. 2008), certain species of dragonfly (personal observation) and certain types of algae (Gebuhr et al. 2006).

Interactions between this phytotelmatous community and *S. purpurea* range from parasitic to mutualistic. Although this relationship was initially believed to be mutualistic (Bradshaw and Creelman 1984), more recent studies have shown that the costs and benefits to each partner depends on which phytotelmatous organism is considered (Mouquet et al. 2008). The mosquito to pitcher plant and bacteria to pitcher plant relationships are more mutualistic than the bacterivore (protozoa and rotifers) to pitcher plant relationship, which was shown to be more parasitic in nature (Mouquet et al. 2008). The life history (Evans 1971, Bergland et al. 2005), thermal and hydric aspects (Kingsolver 1979, Bradshaw 1980, Bradshaw et al. 2000), seasonality (Paterson 1971, Lounibos and Bradshaw 1974, Bradshaw et al. 1998, Rango 1999), and physiology (Bradshaw and Johnson 1995) of members of the phytotelmatous community has been extensively studied. In addition, the interactions among members of the phytotelmatous community (Fish and Hall 1978, Heard 1994a, Cochran-Stafira and Ende 1998, Petersen et al. 2000, Hamilton and Duffield 2002, Miller et al. 2002, Buckley et al. 2003, Trzcinski et al. 2005, Gebuhr 2006, Kneitel 2007, Mouquet et al. 2008, Peterson et al. 2008), and between the phytotelmatous community and *S. purpurea* (Cameron et al. 1977, Heard 1994b, Harvey and Miller 1996, Kneitel and Miller 2003, Hoekman et al. 2007) have also been studied intensely.

Organisms that commonly associate with *S. purpurea* that are not part of the phytotelmatous community include the pitcher plant moths (*Endothenia daeckeana*, *Exyra rolandiana*, and *Exyra semicrocea*), that feed on pitcher tissue (Jones 1904, 1907, 1908, 1935, Schnell 2002). Two species of mite (*Anoetus gibsoni* (Anoetidae) and *Macroseius biscutatus* (Phytoseiidae)) (Nesbitt 1954, Naczi 1986) and a single species of aphid (Robinson 1972) are also known to interact with *S. purpurea*. However, the relationship between mites, aphids, and *S. purpurea* is not well understood (Fashing and O'Conner 1984, Kneitel and Miller 2002). Spiders are also common visitors to *S. purpurea*, but little is known of their interactions (MacBride 1817, Hubbard 1896, Jones 1935, Lloyd 1942, Rymal and Folkerts 1982, Cresswell 1991, 1993, Sudman 1999).

This dissertation research investigated the ecological interactions between spiders and the purple pitcher plant. Spiders can be generalized into two main groupings by their method of prey capture – web-building spiders and ground spiders (Foelix 1996). When selecting habitats, many types of spiders choose areas based on prey density (Waldorf 1976, Riechert 1985, Kareiva et al. 1989, Harwood et al. 2001), vegetation structure (Duffey 1966, Edgar 1971, Riechert 1974, Post and Riechert 1977, Robinson 1981, Halley et al. 1996) vegetation composition (Barnes 1953, Post and Riechert 1977), and abiotic factors such as temperature and humidity (Turnbull 1964, Edgar 1971, Enders 1977, Riechert 1985, Tanaka 1991). Finally, the distribution of spiders is also affected by seasonal changes; population peaks of spiders usually occur in the late spring and early fall (Elliot 1930, Muma and Muma 1949, Barnes 1953).

Certain taxa prefer specific factors over others; for example, members of several wolf spider genera (Lycosidae: a type of ground spider) select foraging locations based on habitat type (Edgar 1971, Kronk and Riechert 1979). Investigations into the role of prey availability in foraging habitat selection by wolf spiders have been met with contrasting results. Wagner and Wise (1997) discovered a correlation to prey availability and *Schizocosa* emigration while, in desert environments, this association was absent (Kronk and Riechert 1979, Wenninger and

Fagan 2000). Competition plays little role in site selection by wolf spiders (Wise and Chen 1999, Wise 1993). Spiders of the family Linyphiidae choose web-sites based on the propensity of having vertical structures to support their webs (Robinson 1981, Samu et al. 1996, Herberstein 1997), the density of prey in the habitat (Wise 1975, Harwood et al. 2001, Harwood et al. 2003), and micro-climate conditions such as temperature and humidity (Samu et al. 1996). Funnel-web spiders (Agelenidae) base their habitat selection on the presence of prey, vegetation structure (Riechert 1974), microhabitat conditions (Foelix 1996), and a natural "spacing" that occurs between spider settlements – a pattern most likely based on prey availability (Riechert 1974).

Spiders use several morphological structures to gather information about their surroundings. A spider's legs contain multiple types of sensory setae. Many setae function as general mechanoreceptors (sensing movement and vibration). Trichobothria, very long setae, are positioned at a more obtuse angle to the exoskeleton and function in sensing air vibrations (Foelix 1996). Slit sensilla near the leg joints measure leg position and cuticle strain, and on the end of legs are chemo-sensitive setae (Foelix 1996). Chemo-sensitive setae have open ends that expose several nerve endings. These endings allow spiders to merely touch a substance in order to "taste" the chemical quality of its surface (Foelix 1996).

Spiders are usually considered generalist predators, or "polyphagous," as they feed on a large variety of prey items; however, insects are their main prey (Foelix 1996). Turnbull (1960) noted that one species of Linyphiidae accepted 98% of the prey items in a laboratory experiment. Most spiders feed on live prey, yet Knost and Rovner (1975) discovered that some members of Lycosidae scavenge for food. Spiders have also been observed consuming nectar. Spider nectivory has been observed in Anyphaenidae, Salticidae, Thomisidae, and Miturgidae (Pollard et al. 1995, Taylor and Foster 1996, Amalin et al. 2001, Jackson et al. 2001, Taylor 2004). Spiders have been observed consuming nectar of *S. purpurea* (personal observation) and *S. flava* (MacBride 1817). Spiders also consume floral nectar (Pollard et al. 1995, Taylor and Foster

1996, Taylor 2004), a substance that has similar ingredients to *S. purpurea* pitcher nectar – mainly amino acids and sucrose (Cipollini et al. 1994, Dress et al. 1997, Deppe et al. 2000). The role spider nectivory plays in the relationship between spiders and *S. purpurea* is unknown.

When living near *S. purpurea*, species of linyphiid spiders have been characterized as being kleptoparasitic (Cresswell 1991, 1993). Lycosid spiders occasionally use the pitchers of *S. purpurea* as oviposition sites (Hubbard 1896, Jones 1935, Rymal and Folkerts 1982). Other unidentified spiders have been hypothesized to have a mutualistic relationship with *S. purpurea* (Schnell 2002).

Kleptoparasitism is an interaction between two or more organisms whereby one or more organisms consumes the prey of another organism (Anderson and Midgley 2002). Hazlett (1981) defined a synonymous term, "resource parasitism", as a positive-negative interaction, whereby the resource-utilization activities of one species has a direct negative effect on another species. Kleptoparasitism is also used by other authors to describe spiders' habits of stealing food from other spiders and birds stealing food from spiders' webs (Wise 1993, Foelix 1996). Cresswell (1991, 1993) studied web-building spiders linyphiid spiders that spun their webs within the aperture of pitchers and robbed those pitchers of insect nutrition. However, the amount of kleptoparasitism that occurred, if any, was not determined and the pitchers were shown not to be significantly affected by this residency. Similarly, the sheet-web weaver, *Frontinella pyramitela* (Linyphiidae), builds webs over the pitchers of *S. purpurea* in New Hampshire, but there is no evidence of kleptoparasitism (Sudman 1999). MacBride (1817) observed that spiders (of an undescribed taxa) attach a string of web to the top of the pitcher to "descend into the tubes, to prey (I suppose) on the entrapped insects". These few studies encompass the breadth of research conducted on the kleptoparasitic relationship between spiders and *S. purpurea*.

Spiders of the families Lycosidae, Linyphiidae, and Theridiidae use *S. purpurea* pitchers as oviposition sites (Hubbard 1896, Jones 1935) and were hypothesized to steal prey in the process (Hubbard 1896). This relationship may be commensal in nature if the spiders receive the

benefit of having a refuge while *S. purpurea* receives no benefit if the pitchers that are being used are already dead.

Evidence of a mutualistic interaction between spiders and *S. purpurea* is non-existent, but has been hypothesized to exist (Schnell 2002). Schnell (2002) postulated that some spiders may be mutualists, as opposed to kleptoparasites (Cresswell 1993), as they may contribute to the plant's health by adding nutrients in the form of their excrement, webbing, and/or dropped insect carcasses. However, no published evidence exists to support this relationship (Newell and Nastase 1998).

Indirect relationships between carnivorous plants and the surrounding macro-invertebrate community are poorly known, but, when studied, often lead to new insights into mutualisms and parasitisms (Anderson and Midgley 2002). For example, new mutualisms involving carnivorous plants have been recently discovered, including one between the carnivorous plant, *Roridula*, and hemipteran insects (Ellis and Midgley 1996) and another between members of the *Nepenthes* genus and certain ant species (Clarke and Kitching 1995). In addition, there are studies that allude to the presence of complex kleptoparasitic relationships in four different systems: spiders, hemipterans, and *Roridula* (Anderson and Midgley 2002); the carnivorous plant, *Pinguicula vallisneriifolia*, slugs and lizards (Zamora 1995); the purple pitcher plant, *Sarracenia purpurea*, and spiders (Cresswell 1993); and *Sarracenia purpurea* and ants (Newell and Nastase 1998). Further research into the indirect relationships of organisms and carnivorous plants have been suggested as a pathway to uncovering the details of how the physiology of carnivory is connected with the specific environmental requirements of carnivorous plants, the constraints of trapping success, and the evolution of plant carnivory (Zamora 1995, Ellison and Gotelli 2001, Anderson and Midgley 2003).

To accurately understand the benefits to carnivory, the environment of the carnivorous plant must be taken into account, including the quantification of indirect relationships (Zamora 1995). Furthermore, when all of the potential costs and benefits of carnivory are taken into

account, a more accurate representation of the advantages to the evolution of carnivory may be developed (Zamora 1995, Mendez and Karlsson 1999). This dissertation examined and quantified the relationship of the carnivorous plant, *Sarracenia purpurea*, with spiders. This relationship was examined as it relates to the unique morphological features of carnivorous plants, spiders' prey capture rates, and the costs and benefits of the relationship to the spider and the plant. The spider diversity and concentration near *S. purpurea* compared to the surrounding environment in addition to the relationship between *S. purpurea*'s unique morphological features and spider occupation was also measured. In addition, this dissertation analyzed the benefits of such a relationship to the spiders as well as possible benefits to the plant in an attempt to categorize the nature of the partnership.

This dissertation attempts to address seven primary hypotheses. The first hypothesis is that *S. purpurea* influences spider abundance and diversity by attracting them to areas of high pitcher plant density. The second hypothesis is that *S. purpurea* influences insect abundance by attracting them to areas of high pitcher plant density. The fourth chapter focuses on the third hypothesis, that the diversity of spiders captured by the plant is similar to that found in the surrounding environment. There are also several other sub-hypotheses discussed in the third chapter: 1) the increased clumping of *S. purpurea* increases the density of spider residents, 2) the increased clumping of *S. purpurea* reduces the capture rate of pitchers, 3) the diversity of spiders captured by pitfall traps will most accurately mimic that of *S. purpurea*, and 4) the most reliable inter-location predictor of spider diversity captured by pitcher plants will be the spider diversity captured by pitcher plants in other environments. The next four chapters each focus on the last four hypotheses: 1) spiders will readily consume *S. purpurea* nectar, 2) arthropod capture and spider residency will be affected by the presence or absence of unique morphological features on pitchers, 3) spiders contribute nutrients to *S. purpurea* pitchers, and 4) that spiders commonly use *S. purpurea* as an oviposition site.

# CHAPTER II

## SPIDER DYNAMICS IN RELATION TO THE ABUNDANCE OF *SARRACENIA PURPUREA*

### Introduction

The purple pitcher plant, *Sarracenia purpurea*, like most other carnivorous plants, is assumed to use nectar and pigment in prey capture (Joel 1986, Juniper et al. 1989, Schnell 2002, Schaefer and Ruxton 2008, Bennett and Ellison 2009). Specifically, these morphological features have been hypothesized to either actively attract prey to the plant or to retain randomly wandering prey on the plant (Juniper et al. 1989, Schnell 2002). However, other studies have revealed that carnivorous plants also rely on random encounters to capture prey (Williams 1976, Zamora 1995). New pitchers, which emerge in the spring (April / May) and fall (Lloyd 1942, Schnell 2002), are much more effective at capturing prey than old pitchers (Fish and Hall 1978, Wolfe 1981, Heard 1998).

Spiders are frequent prey of *S. purpurea* (Lloyd 1942, Wray and Brimley 1943, Judd 1959, Heard 1998). Under the hypothesis that *S. purpurea* actively attracts prey, spiders that are common prey should occur at higher densities near the plant than farther away. If, however, the plant does not lure prey but rather relies on random encounters to catch prey, then spider density near the plant and away from the plant should not differ. These suppositions would also apply to insects that fall prey to *S. purpurea*. Many spiders build webs in regions with high insect densities (Wise 1975, Harwood et al. 2001, 2003). Therefore, if *S. purpurea* does attract prey, the insect density around the plant will be higher than the surrounding areas, and spider density will also be high near the plant.

The main hypothesis of this chapter is that *S. purpurea* influences arachnid abundance and diversity by attracting them to areas of high pitcher plant density. Therefore, arachnid

density in pitcher plant plots will be higher than the arachnid density in non-pitcher plant plots. Furthermore, since diversity would be affected by pitcher plant density, the types of arachnids found in pitcher plant plots will be different than those found in non-pitcher plant plots. Using three different sampling methods, arachnids were collected from vegetation in plots with and without pitcher plants. The numbers of pitcher plants within each treatment plot varied within and among sites. This variability was used to analyze the effect of *S. purpurea* density in addition to absence/presence of the plant. Finally, by identifying spiders and harvestmen, specific taxa were examined for their propensity to be attracted to the plant.

**Methods**

Two locations were considered: the Blackwater Ecologic Preserve (BEP) and Joseph Pines Preserve (JPP). Both BEP (36.87° N, 76.83° W) and JPP (37.05° N, 77.24° W) are in eastern Virginia, (approximately 50 km away from each other). BEP is 319 acres in size, approximately 200 acres larger than JPP. BEP and JPP are fire-dependent communities dominated by turkey oak (*Quercus laevis*) and loblolly pine (*Pinus taeda*), with many herbaceous shrubs and open spaces with low lying plants (Frost and Musselman 1987). Unlike BEP, which is a natural location with approximately 15 – 25 naturally occurring *S. purpurea* clumps, JPP is an artificially managed location, manipulated to have bogs and swales. The 75 *S. purpurea* clumps at JPP were planted in 2003. Both areas are subjected to prescribed burns at least once a year.

The third location had a large planted *S. purpurea* population and was located at the Highlands Biological Station (HBS, 35.05° N, 83.19° W) in North Carolina. This location contained approximately 700 *S. purpurea* plants in an 11 acre botanical garden. The location is not regularly burned.

Plots of 25 $m^2$ were created around all sampled pitcher plants at each location and around areas of similar vegetation that lacked pitcher plants. Similar vegetation structure among plot types was ensured by recording and comparing the density and richness of plant fauna in pitcher

plant versus non-pitcher plant plots. Five plots in pitcher plant areas and five in non-pitcher plant areas were established at BEP (Fig. 1). Two plots of each type were established at HBS and three of each type at JPP (Fig. 1).

Each plot was sampled for spiders and harvestmen using three methods: sweep netting (SN), shrub beating (SB), and pitfall trapping (PT). At BEP, these three techniques were

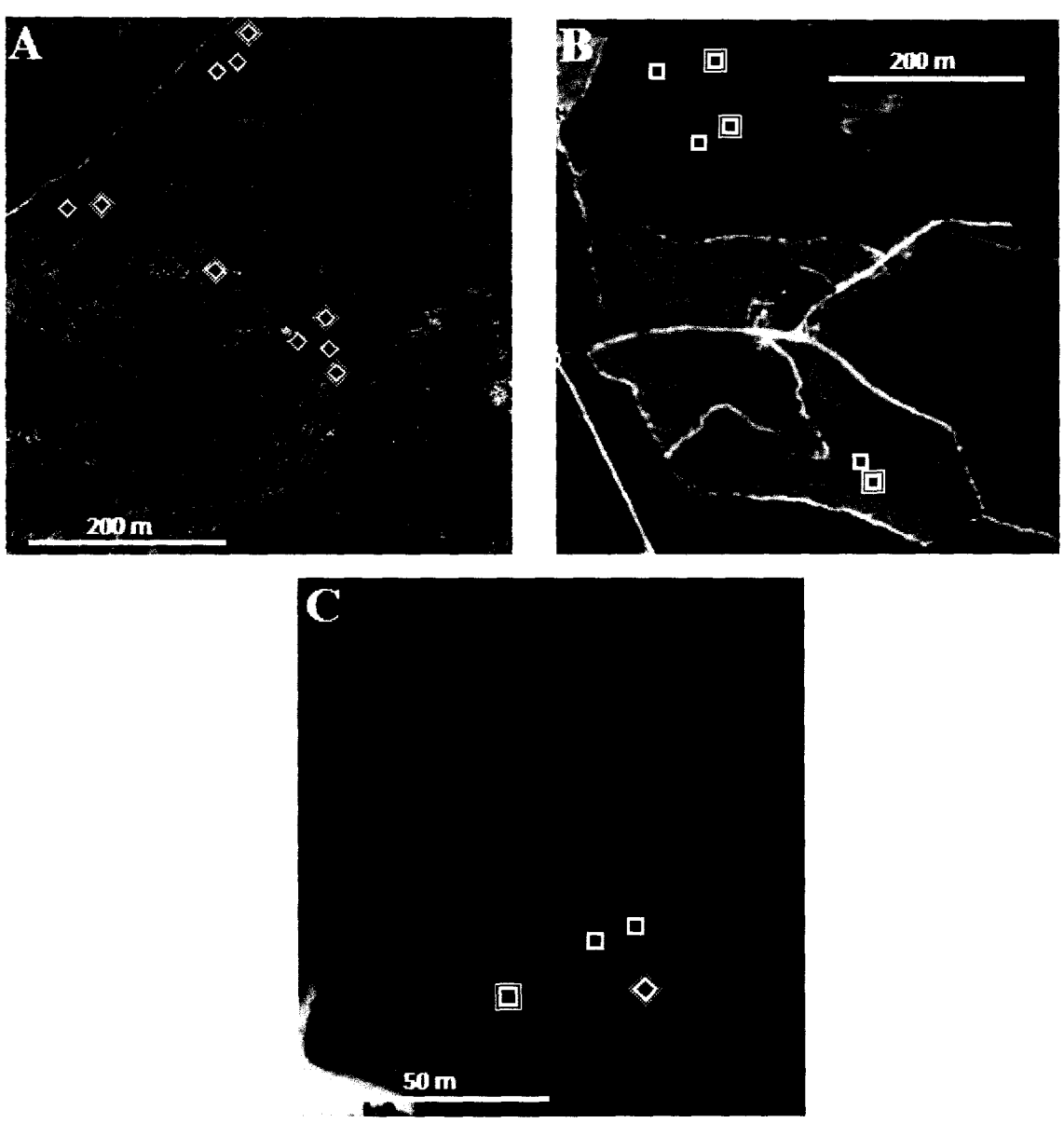


FIG. 1. Aerial photograph of BEP (A), JPP (B), and HBS (C) showing the approximate location of pitcher plant plots (single squares) and non-pitcher plant plots (double-outlined squares).

conducted once every other month for 1 year (N = 60 for each technique). At HBS, environment sampling was performed four times over two months (N = 16, N = 16, N = 80, respectively). Finally, at JPP, pitfall trapping was conducted once a month over six months while sweep netting was done once every other month (shrub beating was not conducted at JPP; PT: N = 180; SN: N = 18).

The technique of SN consisted of waving a sweep net (0.5 m diameter) over grassy vegetation. Four sweeps per 1 $m^2$ section of each 25 $m^2$ plot were conducted. One motion back and forth over a 0.5 $m^2$ area was considered two sweeps. The entire plot was swept unless the vegetation was too large. Large vegetation was sampled with a beating sheet (71 $cm^2$) instead of a sweep net if it had a height of at least 0.25 m and a stem width of less than 3 cm in diameter. However, foliage that had a stem width larger than 3 cm in diameter was considered "tree" and not surveyed. Beating sheets were placed on the ground below each shrub and the shrub was shaken 10 times over the sheet. Pitfall trapping consisted of using 147.9 ml (5 oz) cups filled half-full with soapy water. Each pitfall trap was placed in the ground, flush with the forest floor. Five pitfall traps were placed in each plot. Four of the five pitfall traps were placed at approximately 1 m from each corner of the plot while the fifth pitfall trap was placed at the center of each plot. After one week, the pitfall traps were collected and the arachnids preserved. All arachnids were identified to species using Ubick et al. (2005) and associated taxonomic keys.

Data were tested for normality and homogeneity of variance. If data did not conform to these assumptions, then they were transformed. Alpha was set at $P \leq 0.05$. SN and SB data were combined for most analyses since both were sampling the same vegetation (underbrush).

Hellinger's distance (HD) was calculated using Sørensen's similarity index to determine the difference in vegetation among pitcher plant and non-pitcher plant plots (Sørensen 1948). These statistical procedures were also used to determine the difference in plant communities among the three locations.

Diversity was measured using the Shannon-Weiner index (Zar 1999). Comparisons

among locations in diversity were completed using one-factor ANOVAs (with all collection techniques combined, or each technique independently). Comparisons of diversity between pitcher plant and non-pitcher plant plots at each location were done using independent *t*-tests with a Bonferroni correction (Zar 1999).

Density of arachnids per location was measured by dividing the number of arachnids found at that location by the number of plots sampled at that location. Comparisons of arachnid densities among pitcher plant and non-pitcher plant plots at each location were done with independent *t*-tests with a Bonferroni correction (Zar 1999). A Pearson's bivariate correlation was used to compare the number of pitcher plants found and arachnids captured per plot.

Chi-square tests determined if sex ratios at each location deviated significantly from the expected 50% and if each collection technique produced a significantly different sex ratio than expected. An independent *t*-test compared the maturity ratio between capture techniques. Independent *t*-tests were used at each location to determine if pitcher plant and non-pitcher plant plots differed in the sex ratio or maturity of arachnids found. A one-factor ANOVA determined if there was a significant difference among locations in the ratio of male to female arachnids found and the ratio of adults to spiderlings found.

**Results**

Vegetation was similar between pitcher plant and non-pitcher plant sites at BEP (HD = 0.23) and JPP (HD = 0.30), although less so at HBS (0.5). The similarity in vegetation between sites mirrored the relative distance between the three locations. BEP and JPP were the most similar (HD = 0.56), followed by BEP and HBS (HD = 0.71) and JPP and HBS (HD = 0.82).

During the study 2289 spiders and harvestmen were collected. 1401 arachnids were collected from BEP, 481 from JPP, and 407 from HBS. Various densities of arachnid taxa were found among pitcher plant and non-pitcher plant plots (Table 1). Various densities of arachnid

TABLE 1. Number of spiders and harvestmen collected in non-pitcher plant plots and pitcher plant plots at all three locations. M = male, F = female, and I = immature. Agel = Agelenidae, Any = Anyphaenidae, Aran = Araneidae, Atyp = Atypidae, Club = Clubionidae, Cor = Corinnidae, Cten = Ctenizidae, Cyb = Cybaeidae, Dict = Dictynidae, Erig = Erigoninae, Gna = Gnaphosidae, Hah = Hahniidae, Lin = Linyphiinae, Lio = Liocranidae, Lyc = Lycosidae, Mit = Miturgidae, Mys = Mysmenidae, Opi = Opiliones, Oxy = Oxyopidae, Phil = Philodromidae, Pis = Pisauridae, Salt = Salticidae, Tet = Tetragnathidae, Th = Theridiidae, Tho = Thomisidae, and Ulo = Uloboridae.

| | BEP | | | | | | JPP | | | | | | HBS | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Non-pitcher plant plots | | | Pitcher plant plots | | | Non-pitcher plant plots | | | Pitcher plant plots | | | Non-pitcher plant plots | | | Pitcher plant plots | | |
| Family | M | F | I | M | F | I | M | F | I | M | F | I | M | F | I | M | F | I |
| Agel | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Any | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Aran | 0 | 1 | 26 | 0 | 0 | 39 | 1 | 1 | 20 | 0 | 1 | 14 | 0 | 0 | 6 | 2 | 2 | 10 |
| Atyp | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Club | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 6 | 5 | 5 | 0 | 0 | 1 |
| Cor | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Cten | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Cyb | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Dict | 6 | 0 | 0 | 5 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Erig | 28 | 25 | 82 | 23 | 24 | 95 | 2 | 7 | 4 | 7 | 4 | 8 | 9 | 16 | 4 | 12 | 9 | 3 |
| Gna | 4 | 3 | 9 | 1 | 2 | 12 | 0 | 1 | 2 | 0 | 0 | 7 | 0 | 0 | 0 | 0 | 0 | 0 |
| Hah | 8 | 6 | 2 | 6 | 3 | 0 | 2 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| Lin | 20 | 12 | 3 | 21 | 21 | 8 | 2 | 5 | 1 | 4 | 3 | 4 | 6 | 9 | 6 | 2 | 4 | 6 |
| Lio | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Lyc | 26 | 22 | 275 | 20 | 17 | 233 | 12 | 11 | 92 | 10 | 5 | 42 | 57 | 20 | 52 | 4 | 5 | 25 |
| Mit | 0 | 0 | 10 | 0 | 0 | 6 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Mys | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Opi | 3 | 0 | 20 | 4 | 0 | 15 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 2 | 1 | 1 | 8 |
| Oxy | 1 | 0 | 11 | 1 | 1 | 6 | 0 | 2 | 11 | 1 | 0 | 4 | 0 | 1 | 1 | 1 | 0 | 0 |
| Phil | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Pis | 0 | 0 | 10 | 0 | 0 | 5 | 2 | 0 | 10 | 2 | 0 | 8 | 0 | 0 | 4 | 0 | 0 | 2 |
| Salt | 6 | 2 | 55 | 7 | 5 | 45 | 1 | 7 | 41 | 4 | 7 | 57 | 1 | 2 | 2 | 5 | 9 | 9 |
| Tet | 0 | 0 | 1 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 |
| Th | 1 | 0 | 6 | 1 | 3 | 2 | 0 | 1 | 1 | 0 | 0 | 2 | 5 | 18 | 18 | 1 | 7 | 6 |
| Tho | 1 | 0 | 19 | 2 | 0 | 39 | 1 | 1 | 9 | 0 | 0 | 18 | 0 | 0 | 5 | 1 | 1 | 4 |
| Ulo | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Total | 107 | 73 | 534 | 94 | 77 | 516 | 24 | 38 | 199 | 31 | 21 | 168 | 86 | 73 | 105 | 29 | 40 | 74 |

taxa also existed across all plots at each location (Table 2). Due to differences in the number of plots created at each location, different numbers of arachnids were found. When corrected for the number of plots, BEP and JPP had similar values of arachnids captured per plot, while HBS held a slightly lower arachnid density (Table 2).

Six families/subfamilies of spiders were found exclusively at BEP while one was

TABLE 2. Density and percentage of arachnids captured per family/subfamily, per location. "Other" includes the families Agelenidae, Anyphaenidae, Atypidae, Corinnidae, Ctenizidae, Cybaeidae, Liocranidae, Mysmenidae, Philodromidae, Tetragnathidae, and Uloboridae.

| | BEP | | HBS | | JPP | | Total | |
|---|---|---|---|---|---|---|---|---|
| | # | % | # | % | # | % | # | % |
| Araneidae | 66 | 4.71 | 20 | 4.91 | 37 | 7.69 | 123 | 5.37 |
| Clubionidae | 1 | 0.07 | 17 | 4.18 | 1 | 0.21 | 19 | 0.83 |
| Dictynidae | 11 | 0.79 | 1 | 0.25 | 1 | 0.21 | 13 | 0.57 |
| Erigoninae | 277 | 19.77 | 53 | 13.02 | 32 | 6.65 | 362 | 15.81 |
| Gnaphosidae | 31 | 2.21 | 0 | 0 | 10 | 2.08 | 41 | 1.79 |
| Hahniidae | 25 | 1.78 | 0 | 0 | 8 | 1.66 | 33 | 1.44 |
| Linyphiinae | 85 | 6.07 | 33 | 8.11 | 19 | 3.95 | 137 | 5.99 |
| Lycosidae | 593 | 42.33 | 163 | 40.05 | 172 | 35.76 | 928 | 40.54 |
| Miturgidae | 16 | 1.14 | 0 | 0 | 1 | 0.21 | 17 | 0.74 |
| Opiliones | 42 | 3 | 14 | 3.44 | 3 | 0.62 | 59 | 2.58 |
| Oxyopidae | 20 | 1.43 | 3 | 0.74 | 18 | 3.74 | 41 | 1.79 |
| Pisauridae | 15 | 1.07 | 6 | 1.47 | 22 | 4.57 | 43 | 1.88 |
| Salticidae | 120 | 8.57 | 28 | 6.88 | 117 | 24.32 | 265 | 11.58 |
| Theridiidae | 13 | 0.93 | 55 | 13.51 | 4 | 0.83 | 72 | 3.15 |
| Thomisidae | 61 | 4.35 | 11 | 2.7 | 29 | 6.03 | 101 | 4.41 |
| Other | 25 | 1.78 | 3 | 0.74 | 7 | 1.46 | 35 | 1.53 |
| Total | 1401 | 100% | 407 | 100% | 481 | 100% | 2289 | 100% |
| Plots | 10 | | 4 | | 6 | | 20 | |
| Arachnids/plot | 140 | | 102 | | 80.2 | | 114.5 | |

exclusively found at JPP (Atypidae) and none were exclusive to HBS. In addition, 15 of the remaining 20 families/subfamilies were most often found at BEP. The Clubionidae and Theridiidae were more common at HBS and the Pisauridae were more common at JPP. However, these differences may have been due to more extensive sampling at BEP than the other locations.

TABLE 3. Efficiency of each sampling method over all locations.

| Technique | SN | SB | PT |
|---|---|---|---|
| Arachnids collected | 490 | 324 | 1475 |
| Plots sampled | 20 | 14 | 20 |
| Arachnids / plot | 25 | 23.1 | 73.8 |

Over all locations, PT captured over three times as many arachnids as either SN or SB (Table 3), resulting in a higher efficiency (# of arachnids divided by the number of plots) compared to the other techniques. Different collection techniques also captured different proportions of spider families (Table 4). There was no significant difference in arachnid diversity between locations ($F = 2.28$; $df = 2, 17$; $P = 0.133$).

TABLE 4. Percentage and number of spiders and harvestmen per plot collected in all techniques. "Other" includes Agelenidae, Anyphaenidae, Atypidae, Corinnidae, Ctenizidae, Cybaeidae, Dictynidae, Liocranidae, Mysmenidae, Philodromidae, and Uloboridae. SN = sweep netting; SB = shrub beating; PT = pitfall trapping

| | SN | | SB | | PT | |
|---|---|---|---|---|---|---|
| Family | % | per plot | % | per plot | % | per plot |
| Araneidae | 16.5 | 4.05 | 9.88 | 2.29 | 0.68 | 0.50 |
| Clubionidae | 1.22 | 0.30 | 3.70 | 0.86 | 0.07 | 0.05 |
| Erigoninae | 19.4 | 4.75 | 21.0 | 4.86 | 13.5 | 9.95 |
| Gnaphosidae | 0.82 | 0.20 | 2.78 | 0.64 | 1.90 | 1.40 |
| Hahniidae | 0.00 | 0.00 | 0.00 | 0.00 | 2.24 | 1.65 |
| Linyphiinae | 2.86 | 0.70 | 1.23 | 0.29 | 8.07 | 5.95 |
| Lycosidae | 0.61 | 0.15 | 0.31 | 0.07 | 62.6 | 46.2 |
| Miturgidae | 0.82 | 0.20 | 3.70 | 0.86 | 0.07 | 0.05 |
| Opiliones | 1.43 | 0.35 | 4.32 | 1.00 | 2.58 | 1.90 |
| Oxyopidae | 5.10 | 1.25 | 1.85 | 0.43 | 0.68 | 0.50 |
| Pisauridae | 5.71 | 1.40 | 3.40 | 0.79 | 0.27 | 0.20 |
| Salticidae | 30.0 | 7.35 | 19.8 | 4.57 | 3.66 | 2.70 |
| Tetragnathidae | 1.02 | 0.25 | 0.93 | 0.21 | 0.00 | 0.00 |
| Theridiidae | 6.33 | 1.55 | 11.7 | 2.71 | 0.20 | 0.15 |
| Thomisidae | 6.33 | 1.55 | 14.5 | 3.36 | 1.56 | 1.15 |
| Other | 1.84 | 0.45 | 0.93 | 0.21 | 1.90 | 1.40 |

Separate analyses of PT ($F = 3.03$; $df = 2, 17$; $P = 0.07$) and SN & SB ($F = 0.86$; $df = 2, 17$; $P = 0.44$) data also revealed no significant difference in diversity between locations. There was also no difference in the diversity of arachnids among pitcher plant and non-pitcher plant plots at BEP ($t = 0.01$; $df = 8$; $P = 0.99$), HBS ($t = 3.39$; $df = 2$; $P = 0.08$), or JPP ($t = 0.38$; $df = 4$; $P = 0.73$).

There were various dominant species at each location (Table 5). There was no statistical

TABLE 5. Dominant species at each location and percent of taxa over all locations. Only taxa with at least one dominant species at a single location are shown.

| Family | BEP | HBS | JPP | All | % |
|---|---|---|---|---|---|
| Araneidae | *Mangora gibberosa* | Not applicable | *Gea heptagon* | Not applicable | N/A |
| Clubionidae | Not applicable | *Clubiona rhododendri* | *Clubiona catawba* | *Clubiona rhododendri* | 88.9 |
| Dictynidae | *Cicurina arcuata* | Not applicable | Not applicable | *Cicurina arcuata* | 72.7 |
| Gnaphosidae | *Zelotes duplex* | Not applicable | *Drassylus eremitus* | *Zelotes duplex* | 40 |
| Hahniidae | *Neoantistea agilis* | Not applicable | *Neoantistea agilis* | *Neoantistea agilis* | 100 |
| Linyphiidae | *Lepthyphantes sabulosa* | *Bathyphantes pallidus* | *Erigone autumnalis* | *Lepthyphantes sabulosa* | 24.7 |
| -Erigoninae | *Walckenaeria pallida* | *Ceratinopsis laticeps* | *Erigone autumnalis* | *Walckenaeria pallida* | 10.8 |
| -Linyphiinae | *Lepthyphantes sabulosa* | *Bathyphantes pallidus* | Unidentified *Agyneta* sp. | *Lepthyphantes sabulosa* | 50.6 |
| Lycosidae | *Schizocosa ocreata* | *Pirata insularis* | *Pirata insularis* | *Schizocosa ocreata* | 49 |
| Opiliones | *Vonones sayii* | *Leiobunum ventricosum* | Not applicable | *Vonones sayii* | 38.9 |
| Oxyopidae | *Oxyopes salticus* | *Oxyopes salticus* | *Oxyopes salticus* | *Oxyopes salticus* | 100 |
| Pisauridae | Not applicable | Not applicable | *Pisaurina brevipes* | *Pisaurina brevipes* | 100 |
| Salticidae | *Lyssomanes viridis* | *Pelegrina galathea* | *Thiodina puerpera* | *Lyssomanes viridis* | 38.7 |
| Tetragnathidae | *Leucauge venusta* | *Tetragnatha straminea* | Not applicable | *Tetragnatha straminea* | 100 |
| Theridiidae | *Spintharus flavidus* | *Theridion frondeum* | *Achaearanea conjuncta* | *Theridion frondeum* | 57.1 |
| Thomisidae | *Misumenoides formosipes* | Not applicable | Not applicable | *Misumenoides formosipes* | 23.8 |

difference in the density (arachnids / plot) of arachnids found among pitcher plant and non-pitcher plant plots at BEP (PT: $t = 0.38$; df = 8; $P = 0.72$; SN and SB: $t = 0.54$; df = 8; $P = 0.60$), HBS (PT: $t = 3.77$; df = 2; $P = 0.06$; SN and SB: $t = 0.23$; df = 2; $P = 0.84$), or JPP (PT: $t = 0.33$; df = 4; $P = 0.76$; SN and SB: $t = 0.03$; df = 4; $P = 0.98$). There was no correlation between the

number of pitcher plants found and the density of arachnids captured per plot ($r = 0.257$; $P = 0.474$).

Male and female arachnids occurred at significantly different densities than expected at BEP ($\chi^2 = 21.13$; df = 9; $P = 0.0121$), JPP ($\chi^2 = 23.78$; df = 5; $P < 0.001$), and HBS ($\chi^2 = 13.97$; df = 3; $P < 0.01$) with males being captured more often than females. However, there was no significant difference between pitcher plant and non-pitcher plant plots in the frequency of either sex at BEP ($t = 0.57$; df = 8; $P = 0.59$), HBS ($t = 0.93$; df = 2; $P = 0.45$), and JPP ($t = 0.51$; df = 4; $P = 0.15$). There was also no significant difference among locations in the ratio of male to female arachnids found ($F = 0.014$; df = 2, 17; $P = 0.99$). Different collection techniques produced significantly different sex ratios than expected (PT: $\chi^2 = 104.76$; df = 19; $P < 0.001$; SN & SB: $\chi^2 = 93.65$; df = 19; $P < 0.001$).

There was no significant difference between the density of mature and immature arachnids found in pitcher plant plots vs. non-pitcher plots at BEP ($t = 0.76$; df = 8; $P = 0.47$), HBS ($t = 0.97$; df = 2; $P = 0.44$), and JPP ($t = 1.03$; df = 4; $P = 0.36$). However, between locations there were a significantly greater number of adults at HBS than at other locations ($F = 21.29$; df = 2, 17; $P < 0.001$). PT caught a significantly greater number of adult arachnids per plot than SN & SB ($t = 6.411$; df = 38; $P < 0.001$).

**Discussion**

The morphological features of *S. purpurea* such as nectar and pigment have been hypothesized to actively attract prey, retain prey, or serve both functions (Juniper et al. 1989, Schnell 2002). An active attraction of prey by these features suggests a luring of prey (including arachnids) from outer areas, increasing the density near the plant. However, these results show that arachnid density and diversity are not influenced by the presence of *S. purpurea*.

The active attraction of arachnids as prey by *S. purpurea* would also be affected by the

concentration of morphological features in a given area, in this case represented by an aggregation of plants holding those features. Within this study, pitcher plant plots did not have the same number of plants. In fact, there was a very large difference between pitcher plant plots: both HBS pitcher plant plots contained approximately 100 pitcher plants, JPP pitcher plant plots contained a mean of 11 pitcher plants, and BEP pitcher plant plots averaged approximately three pitcher plants per plot. However, there was no significant correlation between the density of pitcher plants and arachnid density per plot. Zamora (1995) found similar results with the butterwort, *Pinguicula vallisneriifolia*, in rocky habitats of southern Spain: aggregated and solitary *P. vallisneriifolia* captured the same level of biomass, indicating an equal distribution of prey in regions holding both aggregated and solitary plants.

In regards to arachnids as prey, the morphological features of *S. purpurea* may function more in prey retention than attraction (Juniper et al. 1989). A role of prey retention would suggest that pitcher features function to keep arachnids on the pitcher once they randomly encounter the leaf. The hypothesis that these features have a larger role in retention rather than attraction has been shown for other taxa of prey. Williams (1976) found that flying prey land on the sundew, *Drosera intermedia*, just as often as other vegetation. *Drosera intermedia* has no apparent alluring agent, but takes advantage of those prey that randomly land on its leaves. Similarly, Zamora (1995) found that insects had either no preference between landing on the leaves of the carnivorous plant, *Pinguicula vallisneriifolia*, and a non-carnivorous plant, *Potentilla caulescens*, or preferred the latter. If *S. purpurea* uses its morphological features largely for retention rather than attraction, then the density of solitary arthropods such as spiders would not be affected by the plant's density. In contrast, social insects such as ants should increase in density near carnivorous plants since they use their own communication mechanisms to lead their nestmates to the newly found food source (Triplehorn and Johnson 2005). Indeed, ants are the main insect prey of *S. purpurea* (Newell and Nastase 1998, Ellison and Gotelli 2009).

The sex and maturity of captured arachnids were no different in pitcher plant plots than in

non-pitcher plant plots. Although adults were more often captured in PT compared to SN & SB, this result occurred in both plot types. Since adult males wander, looking for mates (Foelix 1996), it is reasonable that PT captured a higher proportion of male arachnids. Similarly, the number of spiderlings captured via PT was inflated due to the large number of lycosid spiderlings found. Lycosid spiderlings cling to their mother's abdomen as first instars (Foelix 1996). Therefore, when a mother with offspring falls into a pitfall trap, all the spiders were captured and recorded. When these spiderling data are removed, the percentage of adult arachnids captured by PT rises from 37% to 72%.

Arachnid density may also be affected by environmental structure. Spiders build webs in regions with greater structural complexity, a phenomenon commonly related to specific plant diversity (Riechert 1974, Post and Riechert 1977, Robinson 1981, Halley et al. 1996). To control for this, non-pitcher plant plots were created in similarly-vegetated regions as pitcher plant plots. The similar Hellinger's distances between plots at BEP and JPP show that pitcher plant and non-pitcher plant plots were similar in their vegetation structure. However, the Hellinger distance of 0.5 at HBS may mean that some variance in arachnid diversity between plots was due to differences in vegetation. The difference in vegetation among locations was correlated to geographic distance between sites whereby closer sites had more similar Hellinger's distance values.

This study presents additional evidence that *S. purpurea* is largely engaged in the selective capture of prey that randomly land on its leaves. Variations in *S. purpurea* density had no effect on arachnid density within pitcher plant plots, either at the same location or across locations.

# CHAPTER III

## INVERTEBRATE DENSITY IN RELATION TO THE CARNIVOROUS PLANT, *SARRACENIA PURPUREA*

### Introduction

Spider prey commonly include small invertebrates such as springtails, aphids, flies, butterflies, beetles, grasshoppers, and other spiders (Foelix 1996). Web-building spiders commonly use the density of these prey to determine the quality of potential web locations (Waldorf 1976, Enders 1977, Riechert 1985, Harwood et al. 2001, 2003). Spiders of the family Linyphiidae are among the groups that commonly use this environmental factor to determine web placement. There are two main linyphiid subfamilies, Erigoninae and Linyphiinae, although a few smaller subfamilies also exist (Miller 2007). Among other differences, the erigonines build smaller webs than the linyphiines (2.8 – 7.5 $cm^2$ vs. 15.9 – 95.0 $cm^2$, respectively: Sunderland et al. 1986a, b, Alderweireldt 1994, Harwood et al. 2001). Moreover, erigonine webs are built closer to the ground than linyphiines (0 – 1.8 cm vs. 3.0 – 10 cm from the ground, respectively: Sunderland et al. 1986a, Harwood et al. 2001).

Individuals of both subfamilies, along with other spiders (personal observation), are common visitors to the purple pitcher plant, *Sarracenia purpurea*. It is currently unknown why spiders are commonly captured by the plant, since spiders are generalist predators (Foelix 1996). Three main hypotheses exist; the first is that spiders visit the plant through the same mechanism as insects, randomly, but are retained by nectar. This hypothesis is corroborated by the presence of spiders as prey inside pitchers (Wray and Brimley 1943, Judd 1959, Heard 1998) and observations of spiders consuming *S. purpurea*-similar nectar in the lab and *S. purpurea* nectar from the plant in the field (personal observation).

The second hypothesis proposes that spiders visit pitcher plants due to their unique

structure (Fage 1928). Evidence supporting this hypothesis includes the observation of spiders of the genus *Agelenopsis* building webs leading into pitchers (personal observation). The final hypothesis is that spiders visit the plant due to a high local insect density. This high density is assumed to be created through the insects' attraction to the plant (Juniper et. al. 1989, Cresswell 1991, 1993, Schnell 2002).

Like most spiders, linyphiids are generalist predators, and feed on insects that are also captured by *S. purpurea* (Wray and Brimley 1943, Judd 1959, Aitchison 1984, Harwood et. al. 2001, 2003). Cresswell (1991) suggested that linyphiid spiders respond to differences in the rate of prey capture by *S. purpurea* by constructing webs near pitchers that capture greater amounts of prey. However, in a later study, Cresswell (1993) measured morphological correlates of prey capture (amount of pigmentation, amount of nectar, pitcher size, etc.) and found that the only positive correlation to spider residency was pitcher height and size. Cresswell (1993) suggested that this was due to the spiders encountering larger and taller pitchers more often due to random spider wandering.

Cresswell (1993) concluded that specific morphological features function as prey attractants, but did not distinguish between attraction and retention. Therefore, it is possible that morphological features correlated with increased prey capture may function in increased prey retention (i.e. the morphological features made the prey stay on the plant once they landed – retention: Juniper et. al. 1989), not necessarily increasing the chance of prey to land (attraction). Additional evidence for the retention rather than the attraction hypothesis can be found by analyzing the frequency of arthropod visitation. Arthropod visitation is not associated with pitcher age or size, temperature, or time of day (Newell and Nastase 1998). Furthermore, these potential prey visit carnivorous plants and the surrounding vegetation at equal frequencies, suggesting a lack of attraction to these plants (Williams 1976, Zamora 1995).

If an attraction to *S. purpurea* exists, it is probable that this attraction would result in an increase in local insect density, and subsequently, spiders may be rewarded by living near the

plant. The main hypothesis of this chapter is that *S. purpurea* attract insects. To determine if living near the plant confers an advantage to spiders, insect density near *S. purpurea* was compared to insect density away from the plant.

**Methods**

The study site was the 319 acre Blackwater Ecologic Preserve (BEP, 36.87° N, 76.83° W) in eastern Virginia. BEP is a fire-dependent community dominated by turkey oak (*Quercus laevis*) and loblolly pine (*Pinus taeda*), with many herbaceous shrubs and open spaces with low lying plants (Frost and Musselman 1987). BEP is subjected to prescribed burns at least once a year and contained approximately 17 *S. purpurea* clumps at the time of sampling (Fig. 2).

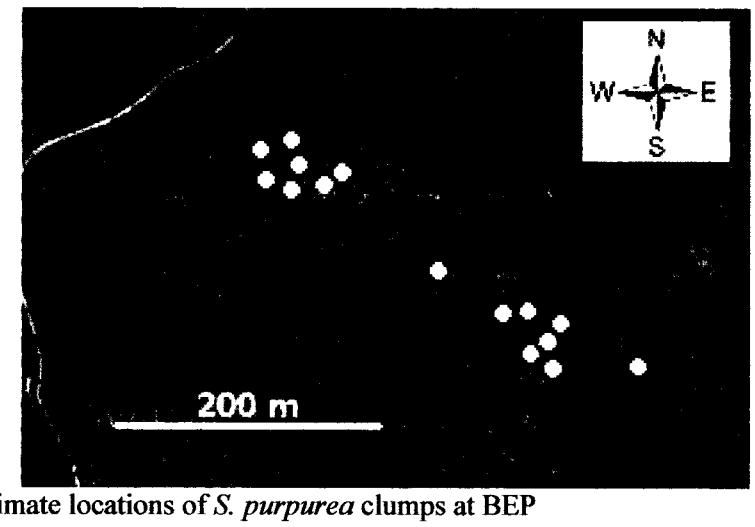


FIG. 2. Approximate locations of *S. purpurea* clumps at BEP

The differences in insect and spider densities were determined for areas adjacent to *S. purpurea* and areas ~2 m from the plant using sticky traps. Two additional variables were used: the height and size of the sticky trap. Trap height consisted of two different sizes: low (3 cm from the ground) and high (10 cm from the ground). These heights are similar to the webs of the two main subfamilies of Linyphiidae. Erigonines build webs that are closer to the ground (0 – 1.8

cm) than the linyphiines (3.0 – 10 cm: Sunderland et al. 1986a, Harwood et al. 2001). Traps consisted of two sizes (15.90 $cm^2$ and 30.18 $cm^2$) of circular, semi-clear pieces of plastic coated on the upper surface with a sticky adhesive glue (Tanglefoot®, Tangle-trap sticky coating, Grand Rapids). Smaller traps were similar to the size of erigonine webs (2.8 – 7.5 $cm^2$) while larger traps resembled linyphiine webs (15.9 – 95.0 $cm^2$: Sunderland et al. 1986b, Alderweireldt 1994, Harwood et al. 2001). Each trap was secured atop a 23 cm wooden dowel with a sewing pin.

All samples were collected during the month of July. Each sampling period lasted two days. Treatment sticky traps were placed adjacent to pitcher plants (<0.1 m away). For small traps, eleven *S. purpurea* were randomly chosen for nearby high trap placement over three sampling periods. Similarly, 13 *S. purpurea* were randomly chosen for nearby low trap placement for large traps over three sampling periods. Small and large traps were put out on different sampling dates (Table 6).

TABLE 6. Experimental setup for treatment traps.

| | | Number of traps placed at BEP | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | 7/12 | 7/14 | 7/16 | 7/18 | 7/20 | 7/22 | 7/24 |
| Small | High | 4 traps | Pickup | 4 traps | Pickup | 3 traps | Pickup | |
| | Low | 4 traps | Pickup | 5 traps | Pickup | 2 traps | Pickup | |
| Large | High | Pickup | 6 traps | Pickup | 6 traps | Pickup | 1 trap | Pickup |
| | Low | Pickup | 9 traps | Pickup | 3 traps | Pickup | 1 trap | Pickup |

During each sampling period (six total), six control traps (three small and three large) set at a high height and two control traps (one small and one large) set at a low height were placed ~2 m away from a randomly chosen subset of those pitcher plants being tested during that sampling period. All captured invertebrates were counted, identified to order, and measured. The size of each arthropod was determined by measuring the length of the organism, from head to abdomen.

Data on insect density per trap and insect length were tested for homogeneity of variances and normality prior to statistical analyses. If data did not fit these parameters, they were

transformed. The total arthropods captured were compared using a one-way ANOVA with a Tukey post-hoc multiple comparisons test. This test was used independently on four more instances to compare the density of dipterans, collembolans, hymenopterans, and coleopterans.

An independent samples *t*-test was used to compare the total number of insects captured by large versus small traps, large high control traps versus large high treatment traps, large low control traps versus large low treatment traps, small high treatment traps versus small high control traps, and small low treatment traps versus small low control traps. Independent samples *t*-tests were used to compare the size of the four most dense orders of prey captured between low and high traps. Bonferroni corrections were done to account for multiple t-tests, resulting in significant $P = 0.0125$.

**Results**

The only significant difference in insect captures was for low control trap types (both small and large) caught significantly more insects than any other trap type ($F = 14.64$; $df = 7, 92$; $P < 0.001$) (Fig. 3). All others compared were not statistically significant. There was no significant difference in the number of dipterans ($F = 1.30$; $df = 7, 92$; $P = 0.26$), hymenopterans ($F = 2.05$; $df = 7, 92$; $P = 0.08$), or coleopterans ($F = 1.31$; $df = 7, 92$; $P = 0.25$) captured among treatment types. However, low control traps caught a significantly greater number of collembolans than any other trap type ($F = 13.89$; $df = 7, 92$; $P < 0.001$) (Fig. 3). There was no significant difference in the number of insects captured between small and large traps ($t = 0.23$; $df = 91$; $P = 0.82$).

There was no significant difference in the number of captured prey between the control and treatment traps placed at high heights for large sized traps ($t = 0.89$; $df = 30$; $P = 0.38$) or small sized traps ($t = 0.94$; $df = 26$; $P = 0.07$). However, control traps captured a larger amount of prey than treatment traps at low heights for the large ($t = 3.01$; $df = 14$; $P < 0.01$) and small trap sizes ($t = 3.75$; $df = 15$; $P < 0.01$).

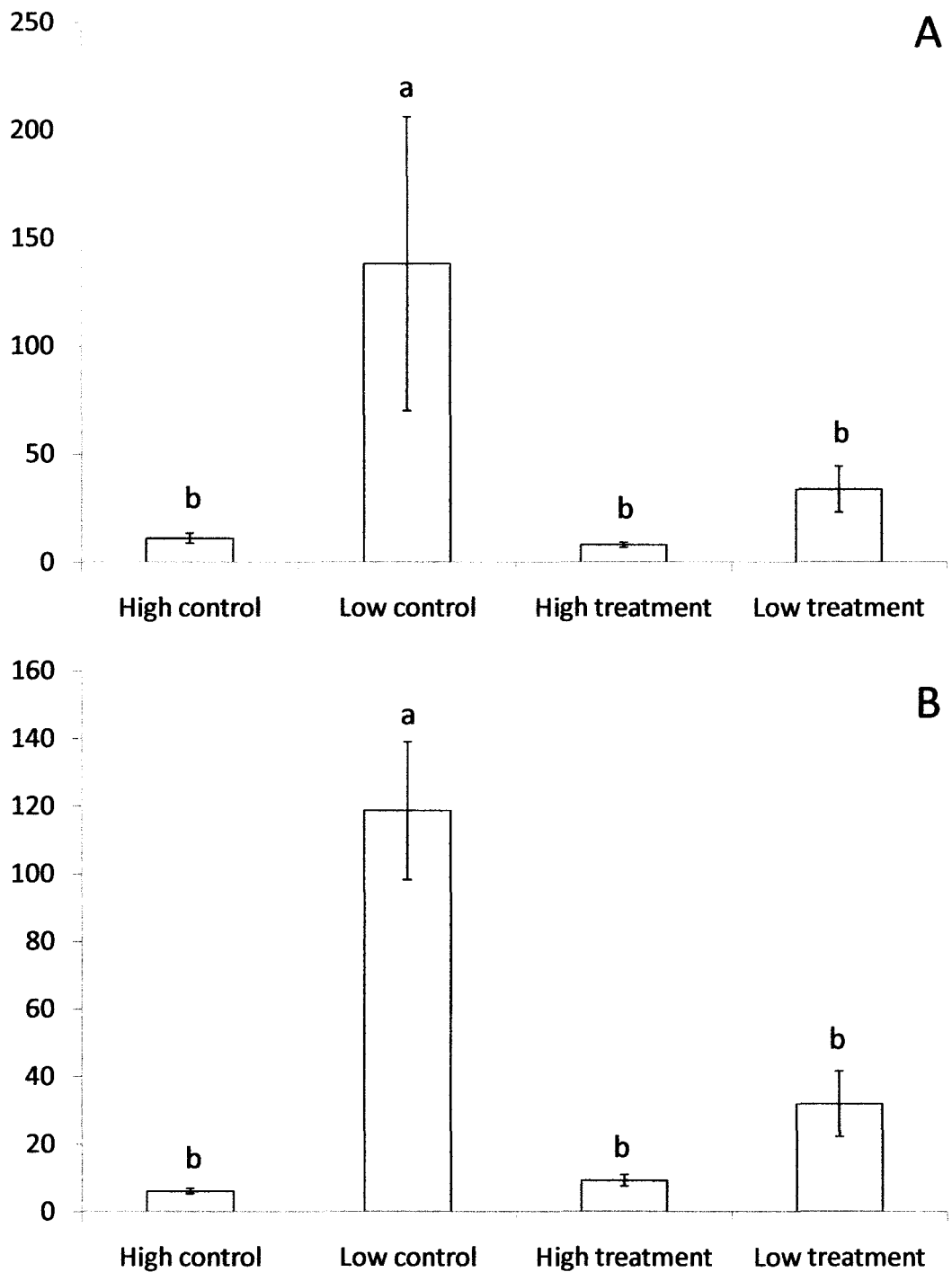


FIG. 3. Mean ± SE number of prey captured per large (A) and small traps (B). Different letters indicate significant differences at $P = 0.05$.

There was a significant difference in the size of the collembolans captured by high and low traps ($t = 7.72$; df = 1807; $P < 0.001$) (Fig. 4). However, there was no significant difference

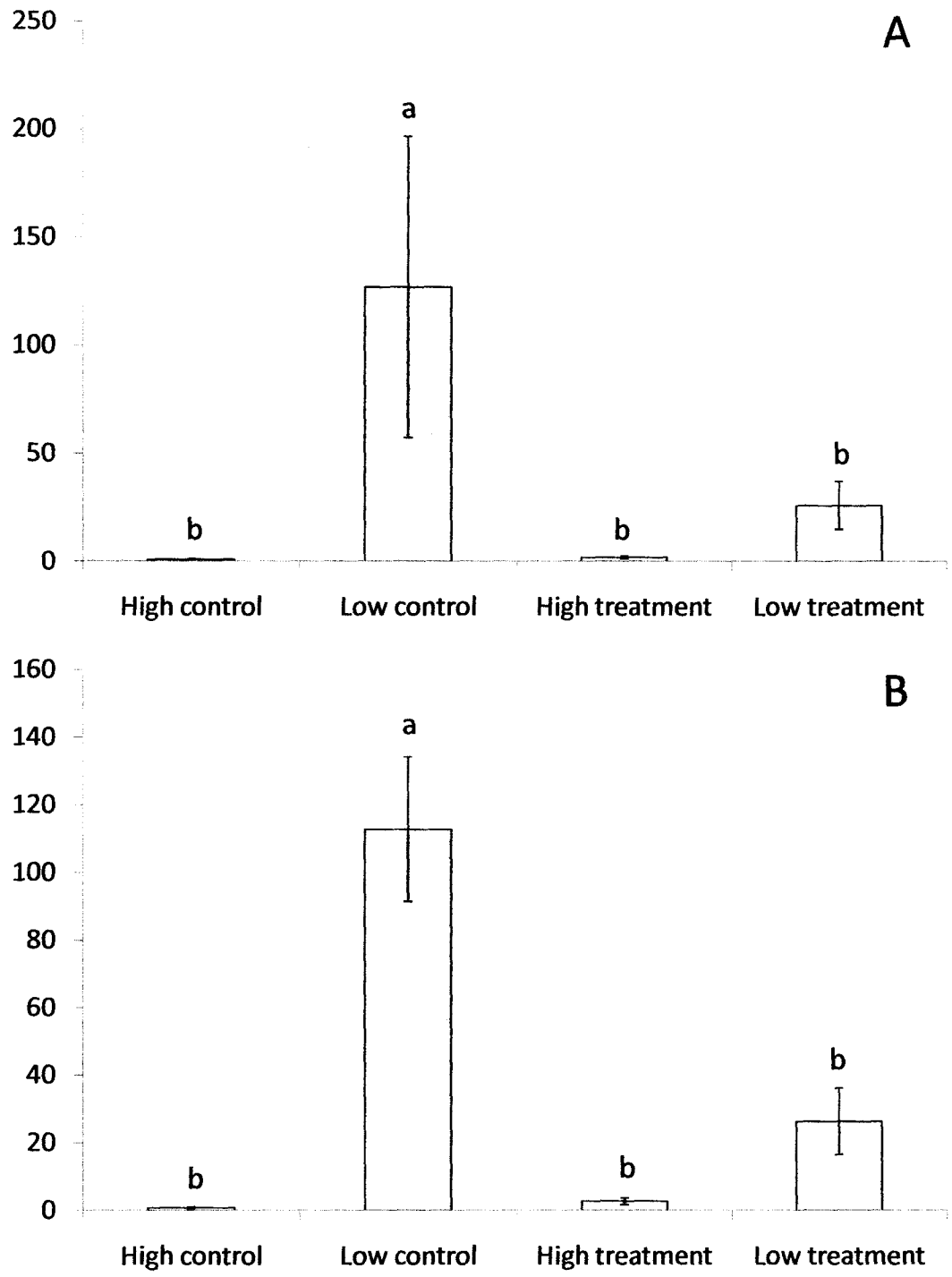


FIG. 4. Mean ± SE number of collembolans captured per large (A) and small traps (B). Different letters indicate significant differences at $P = 0.05$.

in the size of dipterans ($t = 1.94$; df = 680; $P = 0.052$), hymenopterans ($t = 0.40$; df = 95; $P = 0.686$), or coleopterans ($t = 1.56$; df = 56; $P = 0.123$) captured between trap heights (Fig. 5).

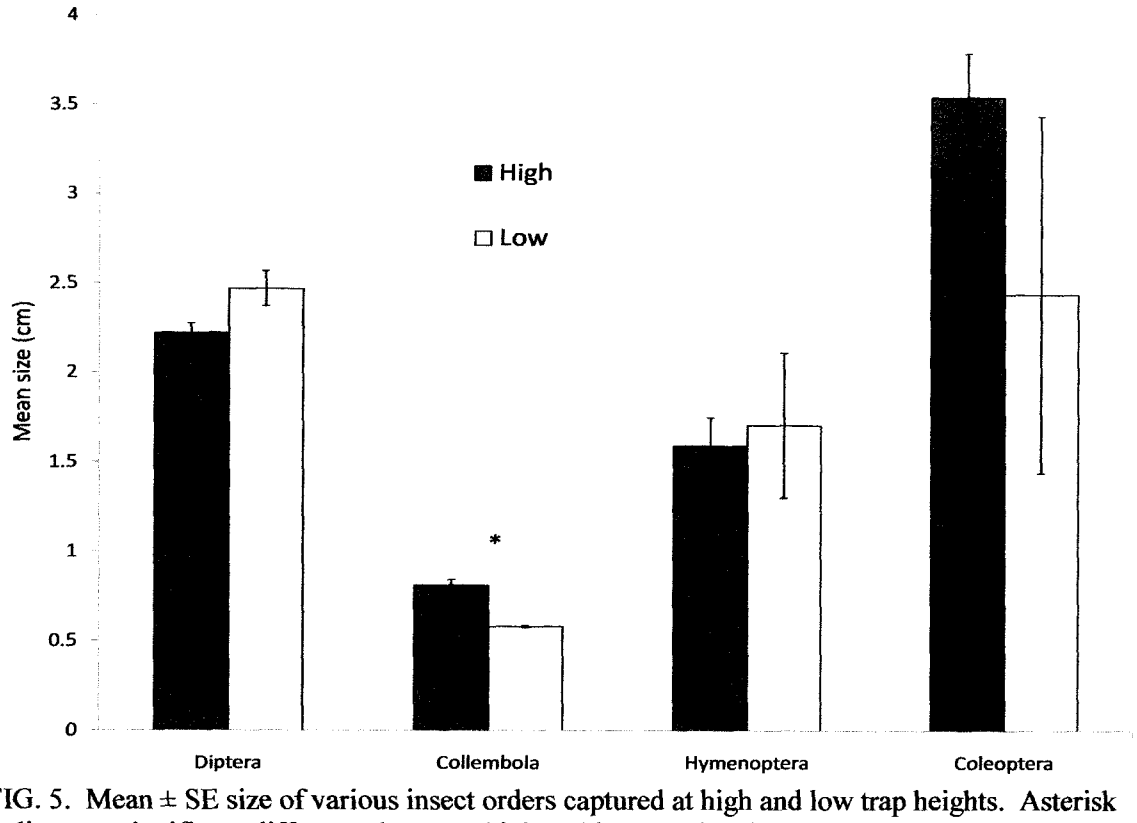


FIG. 5. Mean ± SE size of various insect orders captured at high and low trap heights. Asterisk indicates a significant difference between high and low trap height at $P = 0.0125$.

**Discussion**

These data provide evidence that *S. purpurea* does not attract prey. The similarity in insect density between areas near and far from *S. purpurea* indicates that insects do not congregate near the plant. However, these results may only extend to flying and jumping *S. purpurea* prey due to the collection methods used.

High and low control traps differed only in the density of Collembolans captured, with low traps catching significantly higher numbers than higher traps. This result was also observed by Harwood et al. (2003) when the authors placed sticky traps at low and high heights in fields of winter wheat. Collembolans are soil or leaf litter-dwelling hexapods, common in most temperate environments (up to 100,000 individuals per $m^3$: Triplehorn and Johnson 2005). Most collembolans jump by using a structure on the ventral surface of their abdomen called a furcula. The high capture density of collembolans in low compared to high traps is most likely the result

of their limited jumping height. The lack of a difference between high and low traps in the capture of dipterans, hymenopterans, or coleopterans was not surprising because these insects do not jump and are therefore not present at high densities at 3 – 10 cm above the soil. These data are similar to those of Harwood et al. (2003), in which no significant difference was found in the number of non-collembolan prey between low and high sticky-trap sites.

Collembolans are the most important prey item for linyphiids (Sunderland et al. 1986a), especially erigonines (van Wingerden 1978). By simulating erigonine webs, the low traps revealed that the erigonine behavior of building webs low to the ground is likely to produce a high collembolan capture density. Higher traps that simulated linyphiine webs had a significantly lower collembolan density than lower traps, suggesting that collembolans play less of a role in linyphiine diet than an erigonine diet. However, higher traps captured significantly larger collembolans than lower traps, suggesting that even though higher webs catch less collembolan prey, the collembolans are larger. The larger sized collembolans found in higher traps was most likely a result of these collembolans having larger furcula and therefore a higher jumping height. The similarity in prey size in other orders of arthropods may have been due to a lack of this high soil density or unique jumping behavior. An additional cause may be related to the size of the prey captured – collembolans were much smaller than most other prey types and therefore were easily captured by the sticky traps. Larger prey may have been able to escape the sticky substance on the traps, leading to erroneous capture rates.

Collembolans can be prey of *S. purpurea* (Heard 1998); however their relative numerical capture abundance is dwarfed when compared to almost any other taxon of prey (Ellison and Gotelli 2009). Therefore, although collembolans are numerous at approximately 3 cm above the ground, they are not commonly captured by the plant (pitchers are approximately 10 cm in height). Like many other arthropods, the density of collembolans captured by the plant varies with their density in the environment (Juniper et al. 1989). Although this suggests that collembolan prey capture by *S. purpurea* is random, not all prey show a random capture pattern

(Juniper et al. 1989).

The similarity in prey density between high and low control traps and high and low treatment traps suggests that arthropods do not aggregate near *S. purpurea*. Linyphiid webs near *S. purpurea* may therefore be products of architectural differences with the surrounding environment (pitchers are unique in structure compared to surrounding vegetation) or webs may be randomly placed throughout the environment. Regardless of the cause of spider webs near *S. purpurea*, this study reveals that it is unlikely that spider residency near *S. purpurea* confers an advantage via increased prey density for a spider versus residing in a web on surrounding vegetation.

# CHAPTER IV

## SPIDER INTERACTIONS WITH THE PURPLE PITCHER PLANT, *SARRACENIA PURPUREA*

### Introduction

Arachnids are often captured by carnivorous plants (Wray and Brimley 1943, Ellison and Gotelli 2009), but may also be kleptoparasites of the purple pitcher plant, *Sarracenia purpurea* (Cresswell 1993, Anderson and Midgley 2002). Common prey of *S. purpurea* include insects, spiders, harvestmen, mites, gastropods, and the occasional small vertebrate (Lloyd 1942, Wray and Brimley 1943, Judd 1959, Cresswell 1991, Heard 1998, personal observation). The specific types of arachnids that are captured by pitcher plants are not fully known; Wray and Brimley (1943) recorded nine spiders to family: Araneidae (3), Thomisidae (2), Salticidae (3), and a Lycosidae (1), but left 166 spiders unidentified. However, Wray and Brimley (1943) did not sample the nearby arachnid fauna, thereby excluding a comparison between captured arachnids and local arachnid density. Heard (1998) regrets the lack of data on the surrounding arthropods near his *S. purpurea* populations and notes that the inclusion of such data would have allowed for insights into the differences in prey capture among spatially separated *S. purpurea* populations. In addition, such data could reveal if *S. purpurea* pitchers act as pitfall traps that catch a random subset of the arachnid fauna, or actively lure certain arachnid taxa. Further insights may include differences among arachnids in their tendency to reside (presumably as kleptoparasites) near carnivorous plants.

There are few studies that have examined the ecological interactions between arachnids and *S. purpurea*. Cresswell (1993) examined the frequency of spider residency on pitchers in relation to morphological features of pitchers and found that spider density was correlated with the size and height of the pitcher. However, Sudman (1999) found inconclusive results when

attempting to relate spider residency on pitcher plants to morphological features. Spiders have also been observed to use *S. purpurea* pitchers (Hubbard 1896, Jones 1935) and seed heads (Jennings et al. 2008) as oviposition sites.

This chapter focuses on the hypothesis that the arachnids captured by pitcher plants reflect the diversity of those found in the surrounding environment. Other hypotheses that were addressed include: 1) clumping of *S. purpurea* increases the density of arachnid residents; 2) clumping of *S. purpurea* reduces the capture rate of pitchers, 3) arachnids captured by pitfall traps reflect those consumed by *S. purpurea*; and 4) the arachnid diversity captured by pitcher plants in a given location reflect that which was captured by pitcher plants in other locations.

By sampling captured arachnids found in the pitchers of *S. purpurea* and comparing that diversity to the surrounding environment, the probability of the plant to capture certain arachnid taxa was determined. The diversity of arachnids captured was also compared to the diversity of arachnid residents. Finally, by recording the number of pitchers, the rate of arachnid residency, and the rate of arachnid capture on each clump, the relationship between pitcher aggregation and arachnid residency, capture, and captured arachnid richness was determined.

**Methods**

The two locations in Virginia were the Blackwater Ecologic Preserve (BEP) and Joseph Pines Preserve (JPP). Both BEP (36.87° N, 76.83° W) and JPP (37.05° N, 77.24° W) are located in eastern Virginia, approximately 50 km away from each other. BEP is 129 hectares in size, approximately 81 hectares larger than JPP. BEP and JPP are fire-dependent communities dominated by turkey oak (*Quercus laevis*) and loblolly pine (*Pinus taeda*), with many herbaceous shrubs and open spaces with low lying plants (Frost and Musselman 1987). Unlike BEP, which is a nature preserve with approximately 25 naturally occurring *S. purpurea* clumps, Joseph Pines Preserve is an artificially managed location, manipulated to have bogs and swales and all ~75 *S. purpurea* clumps were planted in 2003. BEP is subjected to prescribed burns at least once a year

while JPP is burned once every other year. The third location was an artificial *S. purpurea* population at the Highlands Biological Station Botanical Garden (HBS, 35.05° N, 83.19° W) in, North Carolina. This unburned location contained over 700 *S. purpurea* in an 11 acre botanical garden.

The location of each *S. purpurea* and the number of pitchers on each plant was recorded for each location (BEP, JPP, and HBS). Due to the nature of *S. purpurea* to propagate via underground rhizomes (Schnell 2002), it was difficult to determine if adjacent whorls were from a single plant or different plants. Therefore, groups of *S. purpurea* were effectively separated into clumps, defined as either a single or multiple whorls of pitchers separated by less than 15 cm.

*S. purpurea* pitchers were sampled to determine the captured arachnids (henceforth, "CC"). At BEP, five pitchers from 20 plants (Fig. 6; n = 100) were sampled approximately every other month for 1 year (September 16, 2006 – June 2nd, 2007; n = 5, N = 500). At HBS, two pitchers from 50 plants (Fig. 7 and Fig. 8; n = 100) were sampled four times over two months (June, 2007 – July, 2007; n = 4, N = 400). At JPP, three pitchers from seven plants and one pitcher from 25 other plants (n = 46) were sampled every month over six months (April, 2008 -

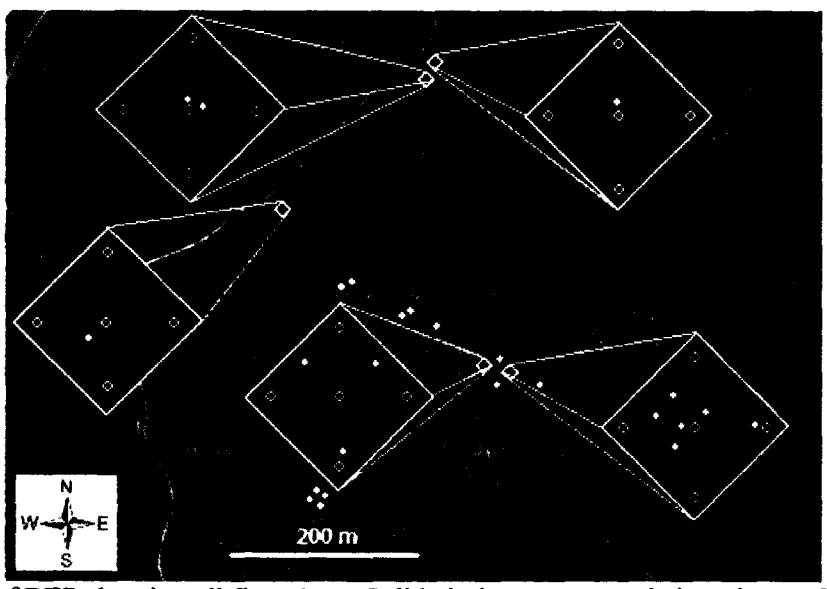


FIG. 6. Map of BEP showing all five plots. Solid circles represent pitcher plants. Open circles represent pitfall traps.

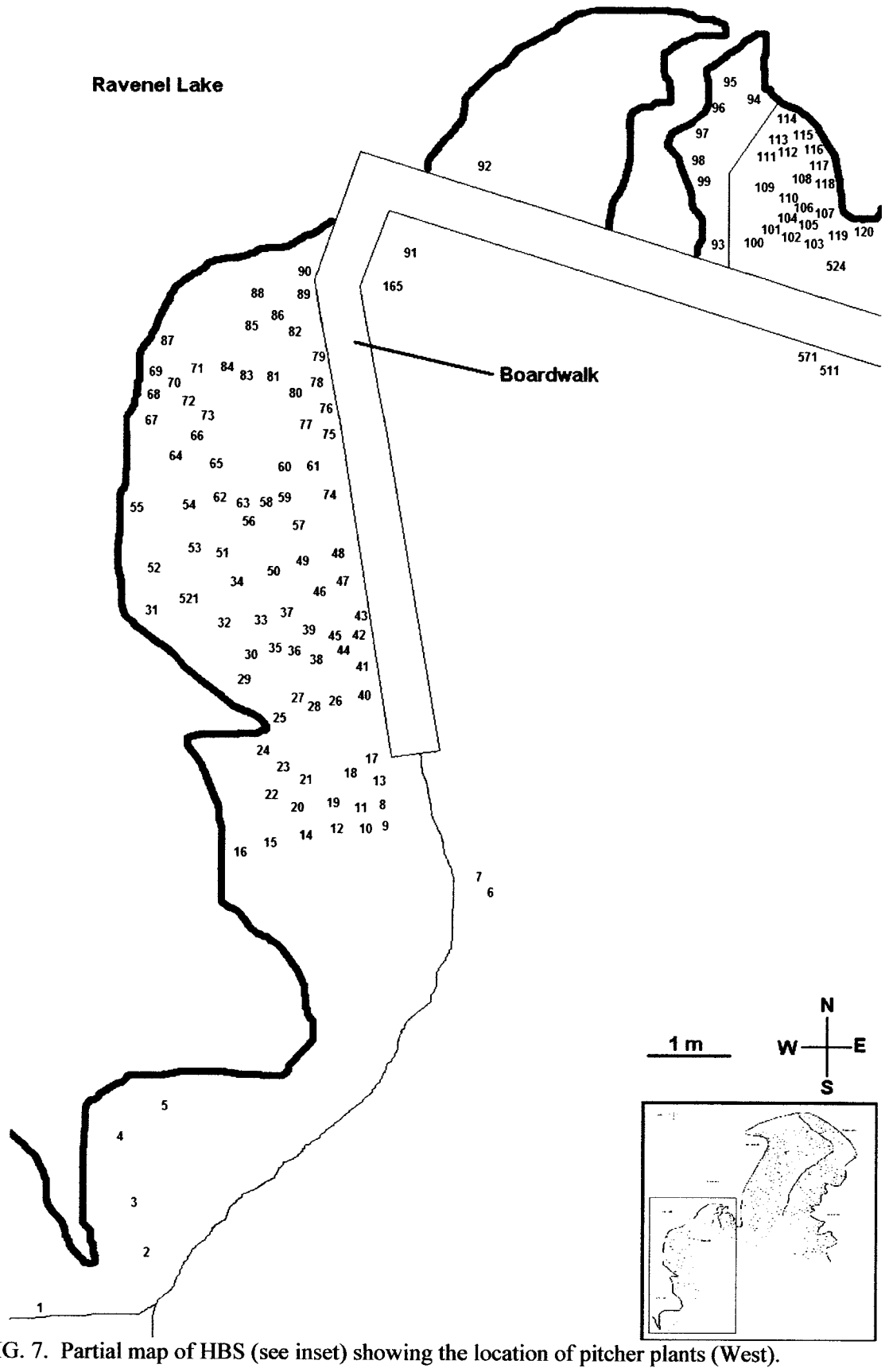


FIG. 7. Partial map of HBS (see inset) showing the location of pitcher plants (West).

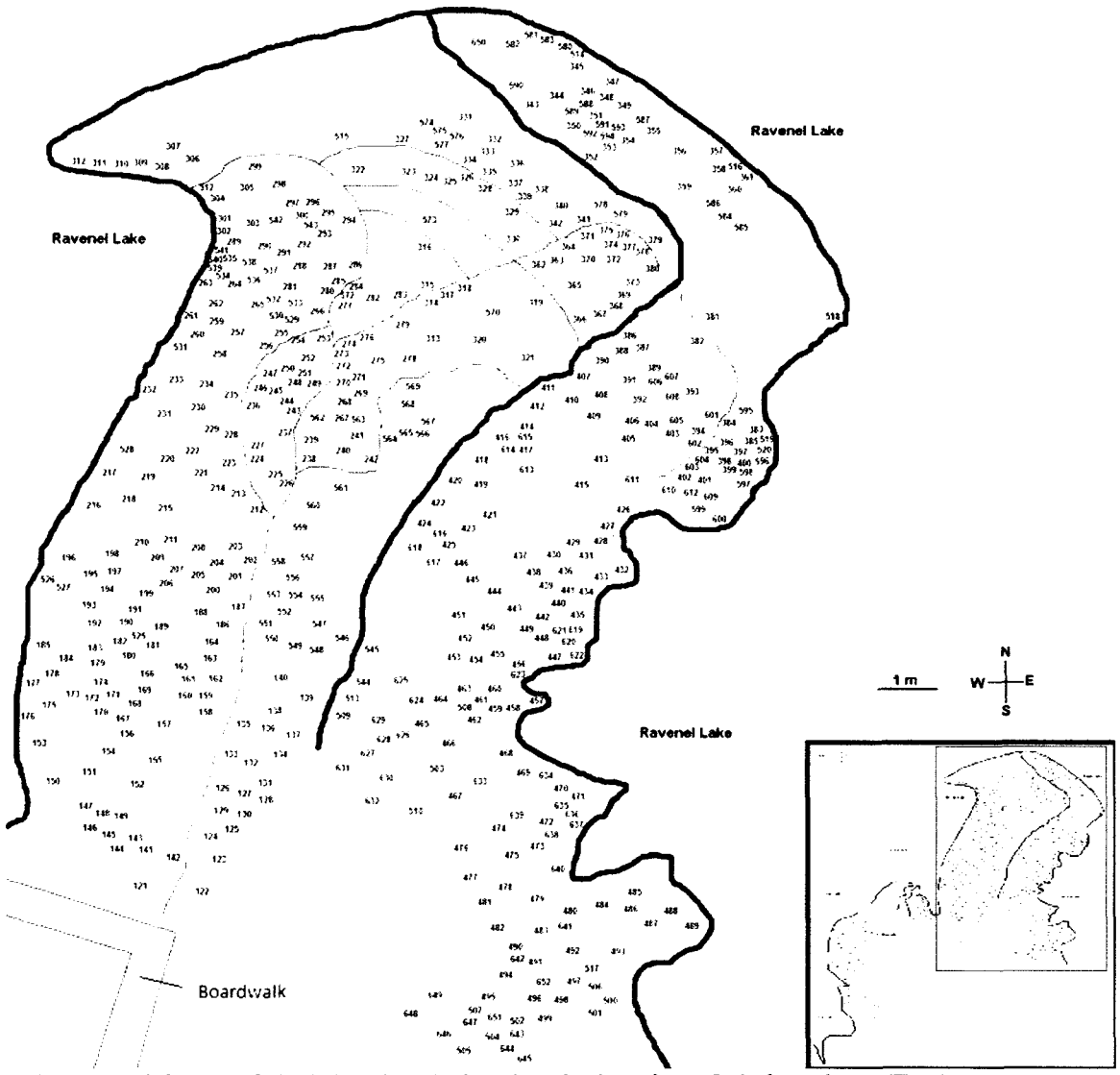


FIG. 8. Partial map of HBS (see inset) showing the location of pitcher plants (East).

September, 2008; n = 6, N = 276; Fig. 9).

Pitchers were sampled by first removing and discarding all liquid and associated prey using a turkey baster and smaller plastic pipettes. They were then given a small mark with a permanent pen to distinguish them from the others. Pitchers were then filled half-full with distilled water and left to catch prey for one week. After one week, all liquid and prey were removed and preserved. Arachnids were later sorted and identified using Ubick et al. (2005).

At JPP and HBS, pitchers were designated as "new" or "non-new" when sampled. New

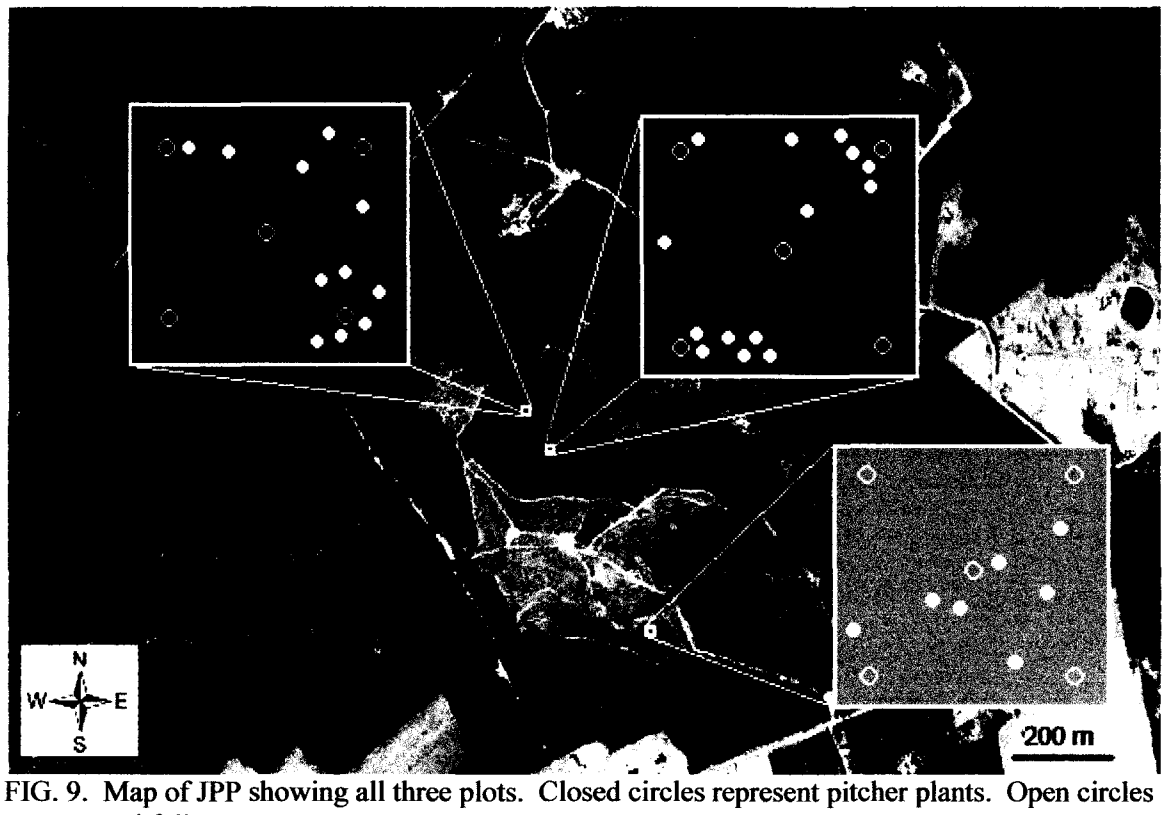


FIG. 9. Map of JPP showing all three plots. Closed circles represent pitcher plants. Open circles represent pitfall traps.

pitchers were identifiable because they emerged during May – July, often lacked high amounts of red pigmentation seen in older pitchers, and had softer tissue than older pitchers (personal observation).

Plants used for sampling through CC were also used to sample resident arachnids. Resident arachnids were collected once a month at BEP (n = 13) on 22 pitchers (n = 22, N = 286). At HBS, ASP was conducted once a week over two months (n = 8) to approximately 130 pitchers during each sampling period (n = 130, N = 1040). At JPP, ASP took place once a month over six months (n = 6) on 32 selected pitchers (n = 32, N = 192).

Plants were checked for arachnid residents through visual inspection. Arachnids were either hand removed or collected using a manual or electronic aspirator (2820A AC Insect Vaccum, Bioquip Products, Inc. Rancho Dominguez, CA). At JPP and HBS, each resident arachnid's position on the plant was recorded as: in a web inside a pitcher, in a web over a

pitcher, in a web that funnels into a pitcher, in a web with an egg sac inside a pitcher, or crawling on a pitcher without a web.

To sample the surrounding arachnid population, 25 $m^2$ plots were created surrounding pitcher plants. Five plots were created at BEP, two at HBS and three at JPP. Each plot was sampled for arachnids using three techniques: sweep netting (SN), shrub beating (SB), and pitfall trapping (PT). Combined, arachnids captured using these techniques were considered arachnids from "the environment".

The technique of SN consisted of waving a sweep net (0.5m diameter) over grassy vegetation. Four sweeps per 1 $m^2$ section of each plot were conducted. One motion back and forth over a 0.5 $m^2$ area was considered two sweeps. Plants that were too large to be sampled by SN were surveyed with beating sheets. Shrub beating used a large canvas sheet (71 $cm^2$). Foliage was considered eligible for SB if it had a height > 0.25 m and a bole width < 3 cm in diameter. Foliage that had a bole width > 3 cm in diameter was considered "tree" and not sampled. Beating sheets were placed on the ground below each shrub and the shrub was shaken 10 times over the sheet. Arachnids were preserved in 80% ethanol. Since both methods sampled arachnids from surrounding vegetation, they were often analyzed together.

Pitfall trapping consisted of using 147.9 ml (5 oz) cups filled half-full with soapy water. Each pitfall trap was placed in the ground, flush with the forest floor. Five pitfall traps were established in each plot. Four of the five pitfall traps were placed at approximately 1 m from each corner of the plot while the fifth pitfall trap was placed at the center of each plot. After one week, the pitfall traps were collected and the arachnids preserved. All arachnids were identified to species using Ubick et al. (2005).

At BEP, sampling was conducted once every other month for 1 year (n = 60 for each technique). At HBS, the sampling occurred four times over two months (n = 16). Finally, at JPP, pitfall trapping was done once a month over six months while sweep netting was done once every other month (shrub beating was not conducted at JPP; PT: n = 36; SN: n = 18). All local

sampling was performed near the same time period as CC and ASP.

Tests for normality and homogeneity of variance were conducted before each statistical study. If data did not conform, data were transformed. All data were considered significant if $P \leq 0.05$. One-factor ANOVAs were used to compare the diversity of arachnids among locations, and among sampling techniques. One-factor ANOVAs with Tukey post-hoc multiple comparisons tests were used to compare the sex ratios and maturity levels of arachnids among locations and techniques. One-factor ANOVAs contrasted the sex ratio and maturity ratio of captured arachnids among the five most common families. Analyses were limited to only five families due to the lack of data found on other arachnid taxa. Sex ratio was calculated as the percent of arachnids in a particular group that were female. Maturity level was calculated as the percent of arachnids in a particular group that were adult.

Correlations were done between densities of arachnids and different techniques at a single location and among the densities of arachnids using a single technique at different locations. Correlations were considered more significant depending on a higher r-value.

The capture rates of new and old pitchers were compared using independent *t*-tests at HBS and JPP. Capture rates were determined by dividing the number of arachnids by the sampling rate of the particular pitcher for each date and location.

Several regression models compared pitchers per clump to: 1) arachnids captured per sample per pitcher; 2) the number of arachnid residents found per sample per pitcher; and 3) the species richness of arachnid prey per sample per pitcher.

The similarity of prey captured by *S. purpurea* (CC) to that collected using PT, SN/SB, or ASP for each location and over all locations was calculated using the Jaccard index (Jaccard 1901). The Jaccard Index ranges from 0 – 1, depending on the number of families shared between both samples.

**Results**

During the course of the study 1,853 arachnids, representing 18 families, were collected (Table 7). Sampling at BEP produced the most samples (Table 7). Arachnid taxa had different

TABLE 7. Density and percentage of arachnids captured per location.

| | BEP | | HBS | | JPP | | ALL LOCATIONS | |
|---|---|---|---|---|---|---|---|---|
| | # | % | # | % | # | % | # | % |
| Agelenidae | 18 | 1.83 | 7 | 1.45 | 2 | 0.52 | 27 | 1.46 |
| Anyphaenidae | 2 | 0.20 | 0 | 0.00 | 0 | 0.00 | 2 | 0.11 |
| Araneidae | 42 | 4.27 | 23 | 4.75 | 26 | 6.74 | 91 | 4.91 |
| Clubionidae | 2 | 0.20 | 4 | 0.83 | 1 | 0.26 | 7 | 0.38 |
| Corinnidae | 6 | 0.61 | 0 | 0.00 | 3 | 0.78 | 9 | 0.49 |
| Dictynidae | 7 | 0.71 | 1 | 0.21 | 0 | 0.00 | 8 | 0.43 |
| Gnaphosidae | 28 | 2.85 | 0 | 0.00 | 14 | 3.63 | 42 | 2.27 |
| Hahniidae | 12 | 1.22 | 0 | 0.00 | 4 | 1.04 | 16 | 0.86 |
| Linyphiidae | 285 | 29.0 | 266 | 54.95 | 86 | 22.28 | 637 | 34.38 |
| -Erigoninae | 194 | 19.74 | 111 | 22.93 | 57 | 14.77 | 362 | 19.54 |
| -Linyphiinae | 91 | 9.26 | 155 | 32.02 | 29 | 7.51 | 275 | 14.84 |
| Lycosidae | 379 | 38.56 | 81 | 16.74 | 111 | 28.76 | 571 | 30.81 |
| Opiliones | 27 | 2.75 | 22 | 4.55 | 2 | 0.52 | 51 | 2.75 |
| Oxyopidae | 11 | 1.12 | 1 | 0.21 | 6 | 1.55 | 18 | 0.97 |
| Pisauridae | 12 | 1.22 | 2 | 0.41 | 12 | 3.11 | 26 | 1.40 |
| Salticidae | 78 | 7.93 | 28 | 5.79 | 85 | 22.02 | 191 | 10.31 |
| Tetragnathidae | 4 | 0.41 | 9 | 1.86 | 0 | 0.00 | 13 | 0.70 |
| Theridiidae | 6 | 0.61 | 34 | 7.02 | 6 | 1.55 | 46 | 2.48 |
| Thomisidae | 49 | 4.98 | 6 | 1.24 | 23 | 5.96 | 78 | 4.21 |
| Other | 17 | 1.73 | 0 | 0 | 5 | 1.30 | 22 | 1.19 |
| Total | 983 | | 484 | | 386 | | 1853 | |
| Samples | 1016 | | 1496 | | 567 | | 3079 | |
| Arachnids/sample | 0.97 | | 0.32 | | 0.68 | | 0.60 | |

rates of capture by *S. purpurea* at each and over all locations (Table 7). In addition, various methods of capture also resulted in location-specific proportions over all locations combined (Table 8). The most commonly found species of each family was also recorded for each location (Table 9).

Seven families/subfamilies of spiders were found exclusively at BEP while none were exclusively found at either of the other locations (Table 7). In addition, nine of the remaining 18

TABLE 8. Percentage and number of arachnids per sample collected in all techniques. "Other" includes Anyphaenidae, Atypidae, Ctenizidae, Cybaeidae, Liocranidae, Miturgidae, Mysmenidae, Philodromidae, and Theridiosomatidae. SN = sweep netting; SB = shrub beating; PT = pitfall trapping; CC = capture composition; ASP = aspirating.

| Family | SN + SB | | PT | | CC | | ASP | |
|---|---|---|---|---|---|---|---|---|
| | % | per sample | % | per sample | % | per sample | % | per sample |
| Agelenidae | 0.00 | 0.00 | 0.16 | 0.00 | 0.37 | 0.00 | 4.80 | 0.02 |
| Araneidae | 14.9 | 0.74 | 0.78 | 0.02 | 1.49 | 0.00 | 3.65 | 0.01 |
| Clubionidae | 0.47 | 0.02 | 0.00 | 0.00 | 0.75 | 0.00 | 0.58 | 0.00 |
| Corinnidae | 0.00 | 0.00 | 0.63 | 0.01 | 1.87 | 0.00 | 0.00 | 0.00 |
| Dictynidae | 0.24 | 0.01 | 0.78 | 0.02 | 0.37 | 0.00 | 0.19 | 0.00 |
| Gnaphosidae | 1.89 | 0.09 | 2.19 | 0.05 | 6.72 | 0.02 | 0.38 | 0.00 |
| Hahniidae | 0.00 | 0.00 | 2.03 | 0.05 | 1.12 | 0.00 | 0.00 | 0.00 |
| Linyphiidae | 22.4 | 1.12 | 25.8 | 0.59 | 41.4 | 0.09 | 51.1 | 0.18 |
| -Erigoninae | 19.8 | 0.99 | 15.9 | 0.36 | 31.3 | 0.07 | 17.7 | 0.06 |
| -Linyphiinae | 2.59 | 0.13 | 9.84 | 0.23 | 10.1 | 0.02 | 33.4 | 0.12 |
| Lycosidae | 0.47 | 0.02 | 56.6 | 1.29 | 29.1 | 0.07 | 24.8 | 0.09 |
| Opiliones | 3.07 | 0.15 | 2.66 | 0.06 | 1.87 | 0.00 | 3.07 | 0.01 |
| Oxyopidae | 1.89 | 0.09 | 0.94 | 0.02 | 0.37 | 0.00 | 0.58 | 0.00 |
| Pisauridae | 3.54 | 0.18 | 0.31 | 0.01 | 0.00 | 0.00 | 1.73 | 0.01 |
| Salticidae | 29.3 | 1.46 | 4.38 | 0.10 | 9.70 | 0.02 | 2.50 | 0.01 |
| Tetragnathidae | 1.18 | 0.06 | 0.00 | 0.00 | 0.00 | 0.00 | 1.54 | 0.01 |
| Theridiidae | 4.95 | 0.25 | 0.16 | 0.00 | 1.49 | 0.00 | 3.84 | 0.01 |
| Thomisidae | 13.2 | 0.66 | 2.19 | 0.05 | 2.24 | 0.01 | 0.38 | 0.00 |
| Other | 2.59 | 0.13 | 0.47 | 0.01 | 1.12 | 0.00 | 0.96 | 0.00 |

families/subfamilies had the highest density per sample at BEP. Over all locations, SN was the most efficient method of capture and CC the least efficient. The number of arachnids found per sample when collecting arachnids through ASP was relatively high at BEP compared to the other locations. However, CC was more efficient at HBS and JPP than BEP (Table 10).

There was also no difference in the diversity of arachnids found over all locations among sampling techniques (SN was combined with SB) ($F = 0.348$; $df = 3, 8$; $P = 0.792$). There was no difference in arachnid diversity in the environment between locations ($F = 1.12$; $df = 2, 7$; $P = 0.378$).

Different collection techniques resulted in different sex ratios (Fig. 10). Across all locations, 43% of the arachnids captured by PT and CC were female, while 53% of the arachnids

TABLE 9. Dominant species and percent of arachnid taxa at each and over all locations. Only families with more than one species at more than one location are shown.

| Family | BEP | % | HBS | % | JPP | % |
|---|---|---|---|---|---|---|
| Araneidae | No dominant species | N/A | No dominant species | N/A | *Gea heptagon* | 93.3 |
| Clubionidae | *Clubiona rhododendri* | 100 | *Clubiona rhododendri* | 100 | *Clubiona catawba* | 100 |
| Corinnidae | *Phrurotimpus certus* | 60 | No dominant species | N/A | *Scotinella madisonia* | 100 |
| Dictynidae | *Cicurina arcuata* | 66.7 | No dominant species | N/A | No dominant species | N/A |
| Gnaphosidae | *Cesonia bilineata* | 33.3 | No dominant species | N/A | No dominant species | N/A |
| Hahniidae | *Neoantistea agilis* | 91.7 | No dominant species | N/A | *Neoantistea agilis* | 100 |
| Linyphiidae | *Lepthyphantes sabulosa* | 28.6 | *Ceratinopsis laticeps* | 29.4 | *Erigone autumnalis* | 21.9 |
| Lycosidae | *Schizocosa ocreata* | 76.5 | *Pirata insularis* | 93.2 | *Pardosa saxatilis* | 19.4 |
| Opiliones | *Leiobunum bimaculatum* | 62.5 | *Leiobunum bimaculatum* | 42.9 | No dominant species | N/A |
| Pisauridae | *Pisaurina brevipes* | 100 | No dominant species | N/A | *Pisaurina brevipes* | 66.7 |
| Salticidae | *Lyssomanes viridis* | 51.2 | *Pelegrina galathea* | 58.8 | No dominant species | N/A |
| Tetragnathidae | *Leucauge venusta* | 100 | *Tetragnatha straminea* | 100 | No dominant species | N/A |
| Theridiidae | *Spintharus flavidus* | 50 | *Enoplognatha caricis* | 44.4 | *Achaearanea globosa* | 100 |
| Thomisidae | *Synema parvulum* | 38.5 | No dominant species | N/A | *Xysticus gulosus* | 50 |

captured through SN + SB were female, and 70% of those captured by ASP were female. These differences resulted in a significantly greater percentage of females than males collected through

TABLE 10. Arachnid numbers per collection technique over all locations. SN = Sweep Netting, SB = Shrub Beating, PT = Pitfall Trapping, CC = Capture Composition, ASP = Aspirating

| Technique | SN | SB | PT | CC | ASP |
|---|---|---|---|---|---|
| Arachnids | 244 | 180 | 640 | 268 | 521 |
| Samples | 47 | 38 | 280 | 1196 | 1518 |
| Arachnids/sample | 5.19 | 4.74 | 2.29 | 0.22 | 0.34 |

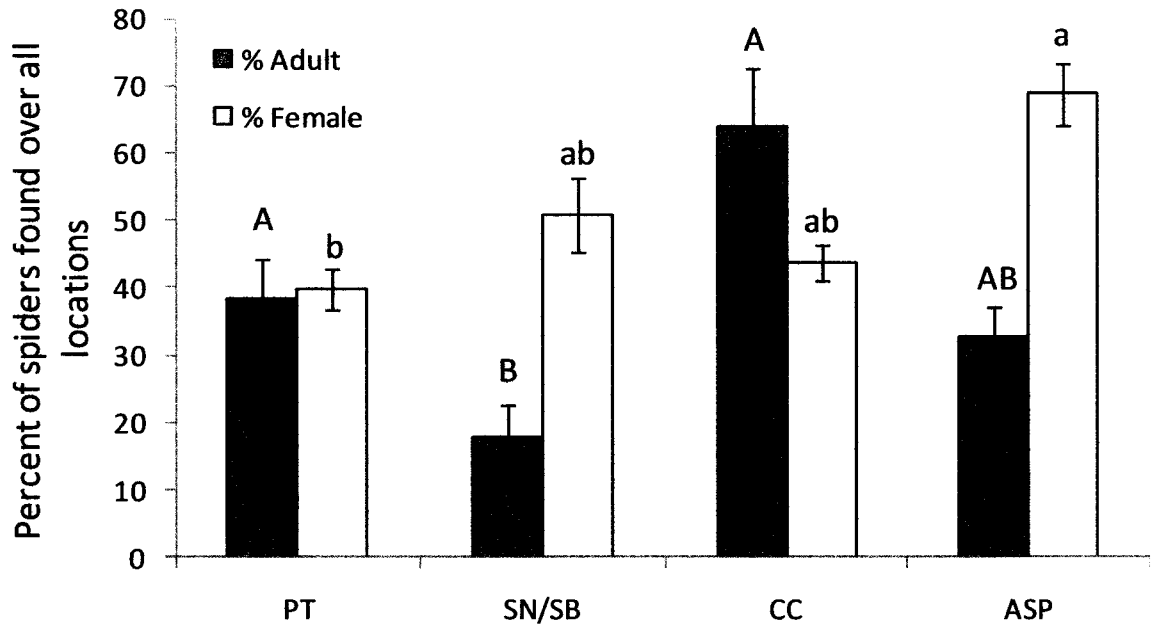


FIG. 10. Mean percentage ± SE of adult and female arachnids captured through each collection technique over all locations. Letters indicate statistically significant differences at $P = 0.05$.

ASP than PT (Tukey's test, $P = 0.013$) ($F = 4.12$; $df = 3, 22$; $P = 0.018$). However, there was no difference among all locations in the ratio of male to female arachnids found in the environment ($F = 2.01$; $df = 2, 7$; $P = 0.204$).

The sex ratio of arachnids also differed by family (Table 11). The sex ratio of arachnids within the five most commonly captured families were significantly different ($F = 5.61$; $df = 4, 14$; $P = 0.012$).

Different collection techniques produced varying maturity ratios (Fig. 10). At all locations, SN + SB captured 17% adult arachnids while ASP captured 34% adult and CC captured 66% adult arachnids. PT resulted in 35% adult arachnids, yet this was mostly due to the large number of lycosid spiderlings captured due to their behavior of traveling on their mother's abdomen; when a young-carrying mother falls into a pitfall trap it takes the young with her, thereby inflating the data. When the lycosid spiderlings were removed from the analysis, PT resulted in 45% adult arachnids. CC and PT captured a significantly larger percentage of adults

TABLE 11. Number of male, female, and immature arachnids captured per family per technique. SN = sweep netting; SB = shrub beating; PT = pitfall trapping; CC = capture composition; ASP = aspirating.

| | SN | | | SB | | | PT | | | CC | | | ASP | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Adult | | I | Adult | | I | Adult | | I | Adult | | I | Adult | | I |
| Family | M | F | | M | F | | M | F | | M | F | | M | F | |
| Agelenidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 23 |
| Anyphaenidae | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Araneidae | 0 | 2 | 40 | 2 | 1 | 18 | 0 | 0 | 5 | 2 | 0 | 2 | 0 | 1 | 18 |
| Atypidae | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Clubionidae | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 2 | 0 |
| Corinnidae | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 2 | 3 | 0 | 0 | 0 | 0 |
| Ctenizidae | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Cybaeidae | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| Dictynidae | 0 | 1 | 0 | 0 | 0 | 0 | 5 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| Gnaphosidae | 0 | 0 | 3 | 0 | 0 | 5 | 1 | 2 | 11 | 1 | 5 | 12 | 0 | 0 | 2 |
| Hahniidae | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 3 | 2 | 3 | 0 | 0 | 0 | 0 | 0 |
| Erigoninae | 0 | 6 | 41 | 4 | 2 | 31 | 38 | 28 | 35 | 42 | 34 | 8 | 11 | 41 | 40 |
| Linyphiinae | 0 | 2 | 6 | 0 | 1 | 2 | 27 | 25 | 10 | 14 | 5 | 8 | 12 | 45 | 117 |
| Liocranidae | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Lycosidae | 0 | 0 | 2 | 0 | 0 | 1 | 34 | 27 | 301 | 20 | 13 | 45 | 5 | 16 | 108 |
| Miturgidae | 0 | 0 | 2 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| Mysmenidae | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Opiliones | 1 | 2 | 2 | 0 | 0 | 8 | 3 | 1 | 13 | 0 | 2 | 3 | 3 | 6 | 9 |
| Oxyopidae | 2 | 0 | 4 | 0 | 0 | 2 | 1 | 1 | 4 | 1 | 0 | 0 | 0 | 0 | 3 |
| Philodromidae | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 |
| Pisauridae | 0 | 0 | 13 | 0 | 0 | 3 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 7 |
| Salticidae | 6 | 6 | 70 | 5 | 9 | 29 | 6 | 6 | 16 | 7 | 8 | 11 | 2 | 1 | 10 |
| Tetragnathidae | 0 | 1 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 |
| Theridiidae | 1 | 2 | 5 | 1 | 8 | 4 | 1 | 0 | 1 | 2 | 2 | 0 | 1 | 18 | 2 |
| Theridiosomatidae | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| Thomisidae | 0 | 0 | 20 | 3 | 1 | 32 | 0 | 0 | 14 | 2 | 1 | 3 | 1 | 0 | 1 |

than SN/SB (Tukey's test, $P = 0.001$ and $P = 0.04$, respectively) ($F = 7.03$; $df = 3, 22$; $P = 0.002$). There was a significantly greater percentage of adult arachnids in the environment at HBS than at other locations, possibly because of the time of sampling (June - July) ($F = 8.27$; $df = 2, 7$; $P = 0.014$).

The maturity ratio of arachnids also differed by family (Table 11). The maturity ratio of arachnids within the five most commonly captured families were significantly different ($F = 4.05$; $df = 4, 14$; $P = 0.033$)

The densities of arachnid taxa captured by CC resembled those of PT compared to the densities found through SB + SN at BEP ($r = 0.90$; $P < 0.001$ and $r = 0.42$; $P = 0.034$, respectively), HBS ($r = 0.94$; $P < 0.001$ and $r = 0.24$; $P = 0.229$, respectively), and JPP ($r = 0.87$; $P < 0.001$ and $r = 0.47$; $P = 0.016$, respectively). The densities of arachnid taxa collected through CC were significantly similar to those captured via ASP at BEP ($r = 0.72$; $P < 0.001$), HBS ($r = 0.79$; $P < 0.001$), and JPP ($r = 0.68$; $P < 0.001$). At a single location, the densities of arachnid taxa captured by pitcher plants (CC) was best explained by PT ($r = 0.92$; $P < 0.001$) followed by ASP ($r = 0.72$; $P < 0.001$) and SN/SB ($r = 0.54$; $P = 0.004$) (Fig. 11).

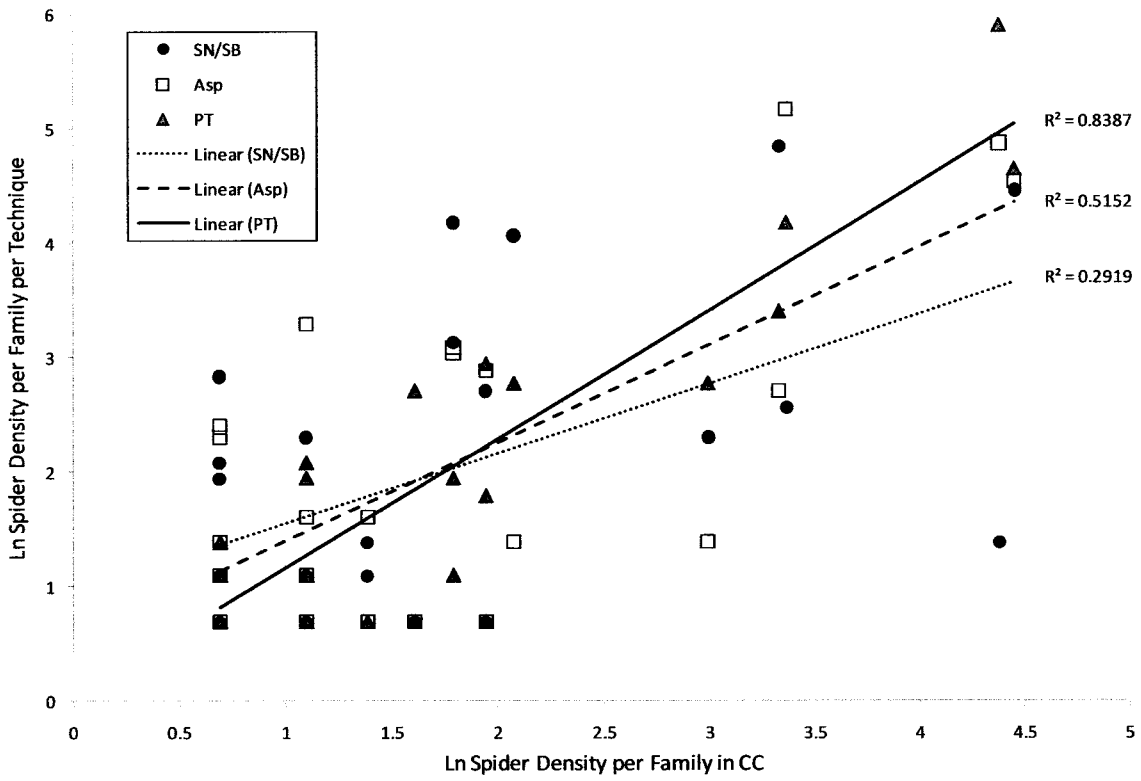


FIG. 11. Correlations between the diversity of arachnid taxa found through various collection techniques at all locations.

When all techniques across locations were compared, the total number of arachnids captured by JPP CC for each family was more similar to BEP CC ($r = 0.94$; $P < 0.001$) and HBS

CC (r = 0.87; $P < 0.001$) than the number of arachnids captured through any other technique at any other location, including those from JPP. The number of arachnids in each family captured through CC at BEP was highly correlated to JPP CC (r = 0.94; $P < 0.001$), and HBS CC (r = 0.87; $P < 0.001$). The number of arachnids in each family captured through CC at HBS was highly correlated to HBS PT, BEP CC (r = 0.87; $P < 0.001$), and JPP CC (r = 0.87; $P < 0.001$). Correlations of the number of arachnids in each family in the environment between locations was either equal to or less than these values for each location (BEP: HBS r = 0.87; $P < 0.001$, BEP: JPP r = 0.76; $P < 0.001$, HBS: JPP r = 0.83; $P < 0.001$).

Similar to CC, the number of arachnids in each family from ASP was more similar to PT than SN + SB at BEP (r = 0.82; $P < 0.001$ and r = 0.28; $P = 0.17$, respectively), HBS (r = 0.68; $P < 0.001$ and r = 0.37; $P = 0.06$, respectively), and JPP (r = 0.76; $P < 0.001$ and r = 0.46; $P = 0.018$, respectively). The number of arachnids in each family captured through ASP across all sites were most similar to CC (r = 0.72; $P < 0.001$) and PT (r = 0.71; $P < 0.001$), and least similar to SN + SB (r = 0.53; $P = 0.005$).

Arachnid density by family was more similar between BEP and JPP for SN/SB (r = 0.77), CC (r = 0.90), and ASP (r = 0.78) than it was between BEP and HBS (r = 0.68, r = 0.77, and r = 0.60, respectively) or HBS and JPP (r = 0.71, r = 0.80, and r = 0.71, respectively). Alternatively , the arachnid density by family caught through PT were most similar between BEP and HBS (r = 0.89) compared to BEP vs. JPP (r = 0.81) or HBS vs. JPP (r = 0.75).

New pitchers captured a significantly greater number of arachnids per pitcher than older ones at HBS ($t = 3.21$; df = 6; $P = 0.018$). However, there was no difference in the number of captured arachnids between new and old pitchers at JPP ($t = 1.71$; df = 6; $P = 0.131$). At BEP, new and old pitchers were marked for only one date (6/2/2007), but on this date new pitchers caught a greater number of arachnids per pitcher than old pitchers (1.02 arachnids per pitcher vs. 0.03 arachnids per pitcher).

A pattern of seasonality existed at each location, but due to differences in the sizes of the

sampling, some locations revealed only a fraction of the larger pattern. The number of arachnids per sample caught by *S. purpurea* (CC) peaked once, in June, at all three locations (Fig. 12). In contrast, the number of arachnids per sample caught by PT peaked in late July at BEP and JPP. However, the numbers of arachnids captured via PT were relatively low at HBS compared to the other locations and did not fit the overall pattern (Fig. 12).

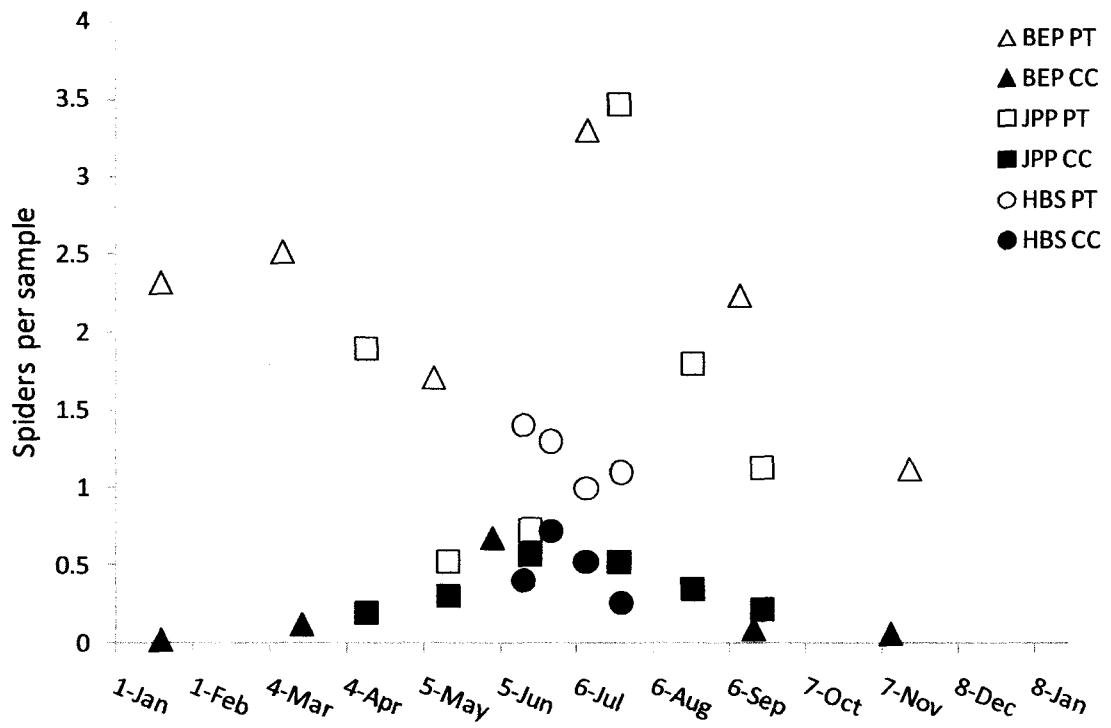


FIG. 12. Seasonality of arachnids per pitcher captured in PT and CC over all locations.

The frequency of arachnid residents found in specific positions in relation to *S. purpurea* pitchers varied across taxa and location. The most common web-building arachnid residents were of the family Linyphiidae (77% of all web-building arachnids collected). 65% were linyphiines and 35% were erigonines. Of all arachnid residents with webs in pitchers, 82% were of the family Linyphiidae over all three locations; of this 82%, 67% were erigonines and 33% were linyphiines. 73% of the linyphiine residents found with webs in pitchers were spiderlings while 46% of erigonines were spiderlings. Of the arachnid residents found with webs over pitchers, the

family Linyphiidae was also the most prominent taxa found (81.3%); within the Linyphiidae, 81% were linyphiines and 19% were erigonines over all locations. However, these relationships were heavily influenced by one location, HBS, from which were collected 89.5% of all resident linyphiides. Linyphiid residents at HBS with webs over pitchers were mostly linyphiines (85.4%) while linyphiid residents at JPP were approximately equally divided between linyphiine and erigonine spiders (43.8% and 56.2%, respectively).

Agelenid spiders, namely *Agelenopsis utahana* and *Agelenopsis kastoni*, were the only taxa found to build webs that funneled into *S. purpurea* pitchers. Whenever these spiders were collected as residents, they were in webs that funneled either into a pitcher or into a crevice between pitchers.

Resident arachnids not found in webs, but found crawling on the plant, were mostly lycosids (68.9% of 45 at JPP and 56.3% of 32 at HBS). A large proportion of non-web-building residents were harvestmen (Opiliones) at HBS (34.5%), less so at BEP (5.6%), and not at JPP (none were found).

Although pitcher aggregation was studied for each location, due to the high number of studied pitcher plants at HBS (~700) compared to BEP (25) or JPP (32), HBS had a much more expansive range of pitcher densities (Fig. 13 and 14). Out of 234 clumps at HBS, clump size ranged from 2 – 2358, with mode = 6 pitchers and mean = 70.75 pitchers. Larger clumps indicated a larger aggregation of pitchers and, therefore, nectar and pigment.

There were significant negative relationships between clump size (number of pitchers) and the number of arachnid residents per pitcher ($r = -0.526$; $P < 0.001$) and between clump size and the number of captured arachnids per pitcher at HBS ($r = -0.374$; $P = 0.001$) via power regression models. However, a relationship was not present at JPP for resident arachnids under any model tested (power $r = 0.105$; $P = 0.66$), but a negative power regression was significant between clump size and the number of captured arachnids (power $r = -0.628$; $P = 0.003$). At BEP, there was no significant relationship between clump size and the number of captured

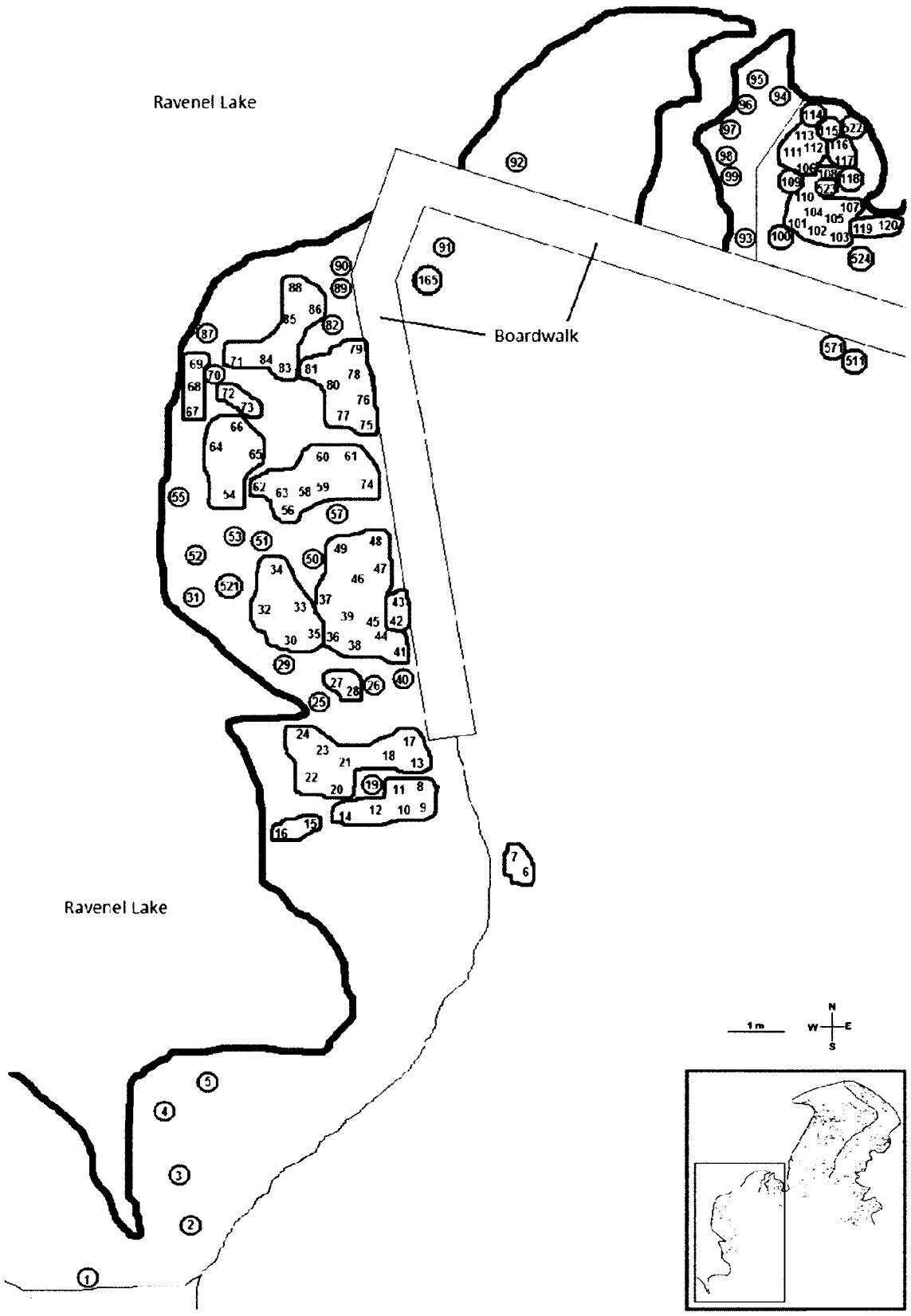


FIG. 13. Partial map (see inset) of pitcher aggregation at HBS (West). Each number represents an individual pitcher plant while each outline represents a clump separated by < 15 cm.

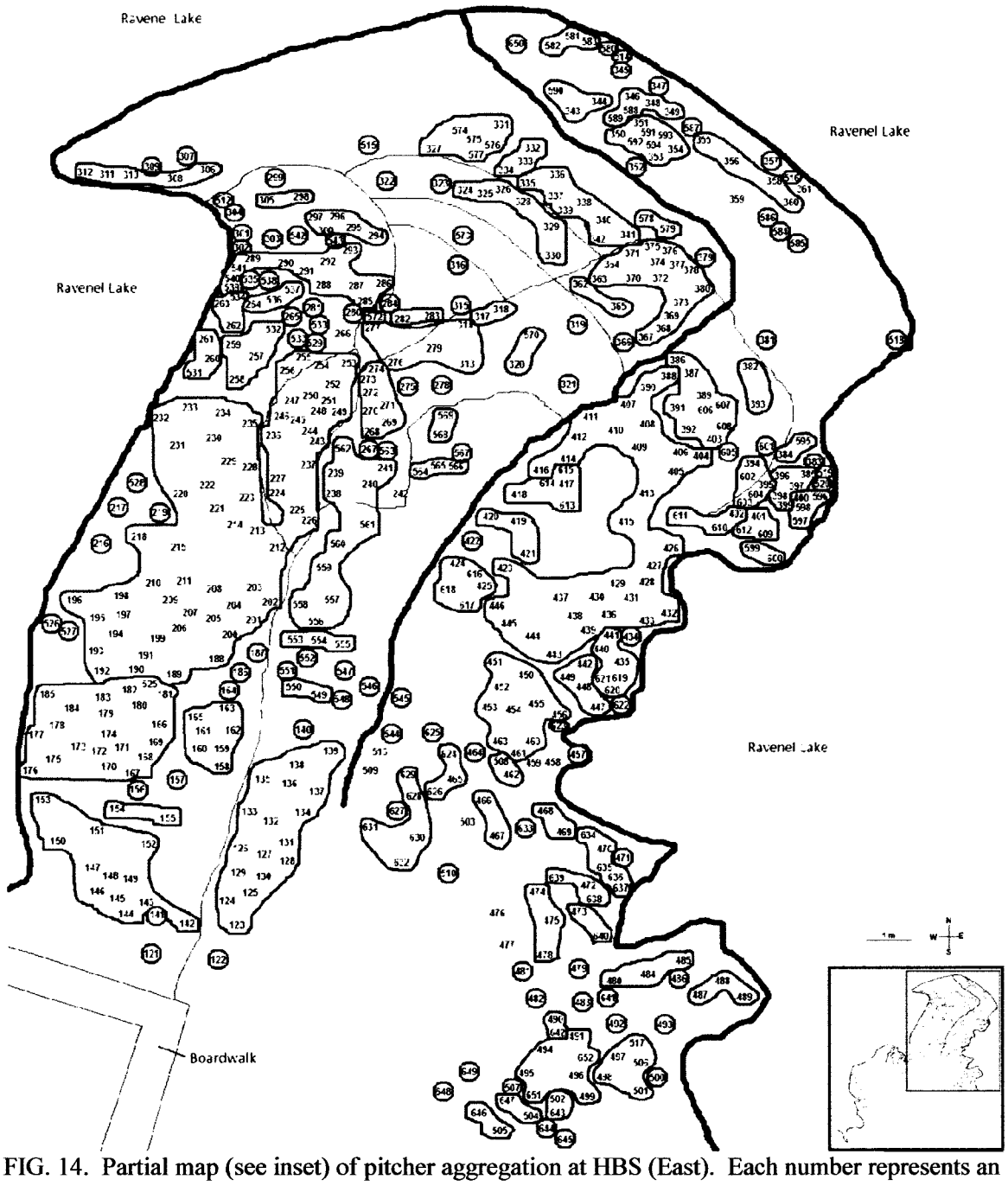


FIG. 14. Partial map (see inset) of pitcher aggregation at HBS (East). Each number represents an individual pitcher plant while each outline represents a clump separated by < 15 cm.

arachnids per pitcher under any model tested (linear r = -0.395; $P = 0.106$) but a significant negative linear relationship did exist between clump size and the number of residents per pitcher (linear r = -0.650; $P = 0.003$). When all data were combined from all locations for each analysis,

there was a significant negative power relationship between clump size and the number of arachnid residents per pitcher (r = -0.525; $P < 0.001$) and between clump size and the number of captured arachnids per pitcher (power r = -0.407; $P < 0.001$) (Fig. 15). There was a significant negative power relationship between clump size and species richness at HBS (power r = -0.435; $P < 0.001$), JPP (power r = - 0.659; $P = 0.002$), and BEP (power r = -0.50; $P = 0.035$). There was a significant negative power relationship when data from all sites were combined (r = -0.439; $P < 0.001$) (Fig. 15). Therefore showing that as clump size increased, the diversity of species captured decreased.

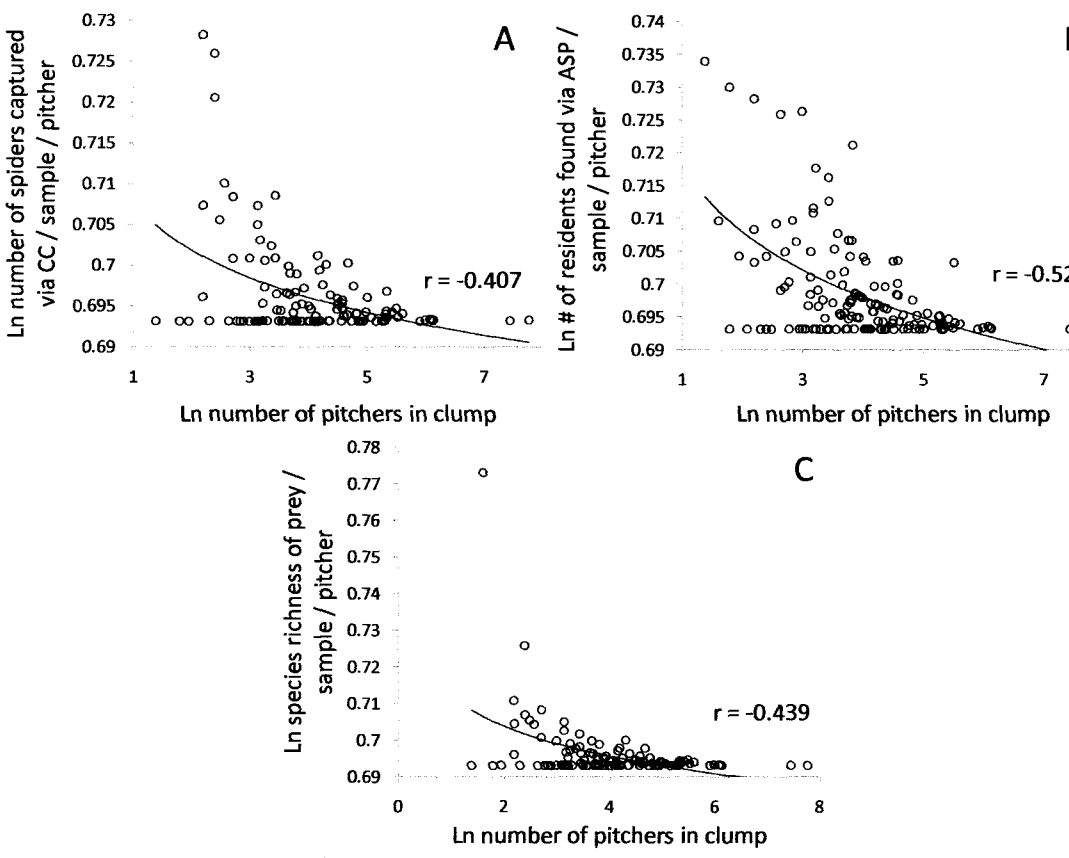


FIG. 15. Negative power relationships between clump size and a) the number of arachnids captured via CC / sample / pitcher, b) the number of arachnid residents collected via ASP / sample / pitcher, and c) species richness over all locations.

**Discussion**

Several novel conclusions can be drawn from these data. Distinct differences existed between arachnid taxa, males and females, and adults and spiderlings in their tendencies to be residents or prey of *S. purpurea*, and these differences were not always tied to their density in the environment. New pitchers often captured more arachnids than old pitchers, suggesting a response by arachnids to pitcher morphological features. The most accurate collection technique at predicting the density of arachnid taxa captured in pitcher plants within the same location was pitfall trapping. The most accurate collection technique at predicting the arachnid diversity captured in pitcher plants among different locations was capture composition, suggesting that although arachnid diversity varied in the environment, *S. purpurea* captured relatively the same taxa. The tendency of arachnid residency was a relatively accurate predictor of the probability of becoming a victim of *S. purpurea.* Negative power relationships existed between the number of pitchers in a clump and the number of arachnid residents, the number of captured arachnids, and the species richness of captured arachnids.

There were differences among arachnids in their tendencies to be residents or prey; ground spiders such as lycosids, gnaphosids, and salticids were more common as prey while web-building spiders of the subfamily Linyphiinae were more often residents. Linyphiids were the most common residents, with the linyphiines more common than the erigonines. The percentage of erigonine residents was similar to their proportion found by SN/SB or PT, but the linyphiines were far more common as residents than would be expected given the proportion of linyphiines found in SN/SB or PT. Linyphiids choose websites based on many factors, including the presence of vertical structures to support their webs (Robinson 1981, Samu et al. 1996, Herberstein 1997). Many linyphiids built webs inside *S. purpurea* pitchers, structures that form cavities with high vertical walls. The most common builders of webs inside pitchers were mature erigonines and linyphiine spiderlings. Erigonines are smaller than linyphiines and commonly build smaller webs (Sunderland et al. 1986b). Adult erigonines commonly build webs of 3 $cm^2$

(Sunderland et al. 1986a) - 8 $cm^2$ (Harwood et al. 2001), a range similar to the mean area inside a random sampling of *S. purpurea* pitchers (7.69 $cm^2$) (Milne *unpublished data*). Adult linyphiines build webs from 16$cm^2$ (Sunderland et al. 1986a) - 74$cm^2$ (Harwood et al. 2001). Since web size increases as spiders age (Riechert et al. 1973, Riechert 1974, Risch et al. 1977, Robinson and Lubin 1979), the smaller webs of linyphiine spiderlings were probably more suitable for *S. purpurea* pitchers than adult linyphiine webs.

Agelenid spiderlings were commonly collected with webs leading into pitchers and were almost never captured in the environment. Agelenids often seek out vegetation that helps to build their funnel webs (Foelix 1996), and *S. purpurea* pitchers would provide a suitable web location. Since the size of most spiders' webs is proportional to the age of the spider (Witt et al. 1972), the size of *S. purpurea* pitchers is presumably large enough for immature funnel weavers, but too small for adult agelenids. Unlike the linyphiids and other web-building residents, agelenid webs often spanned multiple pitchers, making it unlikely for prey to enter them.

Over 40% of all arachnids captured by *S. purpurea* were of the family Linyphiidae. Most of these were of the subfamily Erigoninae, while arachnids of the subfamily Linyphiinae were less likely to be captured. Captured linyphiines constituted approximately the same proportion that were found in pitfall traps, but the erigonines made up a larger percentage of captured arachnids than their proportion collected through either PT or SN/SB. The high capture rate of erigonines may be tied to their tendency to reside inside of *S. purpurea* pitchers. Erigonines may then easily become prey due to slips along the smooth inner surface of the pitcher. Since erigonines are more prone to hunt for prey at the edges of their web compared to linyphiines (Harwood et al. 2003), this behavior may have contributed to accidental falls into the pitcher depths. In addition, larger prey falling into or struggling within the pitcher may catch the web and bring the spider along with it. However, linyphiine spiderlings commonly built webs inside *S. purpurea* pitchers, but were less often captured by the plant than adults. Other factors, such as the propensity to consume *S. purpurea* nectar, may explain the higher incidences of erigonine

capture by pitchers.

The second most common prey of *S. purpurea* were lycosid spiders, which encompassed approximately 29% of captured arachnids. However, first instar Lycosidae ride on their mother's back for seven to eight days after hatching (Foelix 1996), and when the mother is captured by a trap (PT or CC), the spiderlings fall victim too, thereby inflating the numbers. The other commonly captured taxa were also non-web building arachnids: salticids, gnaphosids, thomisids, corinnids, and harvestmen (Opiliones). The high capture density of these taxa was largely correlated to their high prevalence in the environment, but this does not explain their disproportionate capture by new pitchers. These arachnids commonly wander along the ground, searching for food. In addition, adult male spiders commonly wander great distances looking for females (Foelix 1996). Their capture by new pitchers may be due to one of, or a combination of, the following: a tendency for males to wander, contact, and fall into pitchers more often, a tendency to drink nectar once it is serendipitously discovered upon wandering, and/or an attraction to a commonly present morphological feature such as a UV pattern or fragrance. Spiders readily drink sugar-laden liquids and nectar similar to *S. purpurea* nectar (Cipollini et al. 1994, Dress et al. 1997) in the laboratory (Pollard et al. 1995, Amalin et al. 2001, Jackson et al. 2001, Taylor 2004) and appear unaware of its presence until contact is made (Milne *unpublished data*). These data suggest that arachnids may not be lured by nectar from afar, but rather, become prey due to their behavior upon the serendipitous discovery of nectar. Some spiders can see in the UV spectrum (Yamashita and Tateda 1976, Lim and Li 2006) so it is also possible that spiders are attracted to pitchers with UV patterns.

Since new pitchers emerge and open in early May and are most efficient at prey capture between 10 – 20 days after opening (Fish and Hall 1978), *S. purpurea* captures prey that is active from mid-May through the fall, when new pitchers are constantly emerging. Since most *S. purpurea* prey are ants, it would be expected that these pitchers open at the same time that ants are active, and this is indeed the case (Triplehorn and Johnson 2005). However, arachnids also

make up a considerable portion of *S. purpurea* prey (Wray and Brimley 1943, Rango 1999, Heard 1998). A large majority of arachnids were in high abundance in the environment during the summer at all of the locations, especially the ground arachnids. Yet, the araneids and linyphiids had large density peaks in the winter and summer, suggesting that pitcher opening is not correlated with the densities of these arachnids.

Of the four types of capture techniques used, PT produced arachnid densities that were the most similar to the arachnid densities captured by *S. purpurea* (CC) at each site. This was expected because pitfall traps function in a similar manner to *S. purpurea* pitchers by being low to the ground through the use of a pitfall mechanism. However, in other ways, this similarity was unexpected; pitfall traps function at random while *S. purpurea* is thought to use features such as nectar and pigment to catch prey. Therefore, the high similarity between PT and CC suggests that arachnid capture by *S. purpurea* occurs at random, much like a pitfall trap. However, new pitchers captured more arachnids than older pitchers, suggesting that *S. purpurea* retains or attracts arachnids more effectively than older pitchers. Since the main difference between new and old pitchers is the amount of nectar produced (Fish and Hall 1978, Bennett and Ellison 2009), nectar may play a large role in this retention / attraction process. Moreover, the truth may lie between these two hypotheses: arachnids may become prey of serendipitous discoveries of nectar and/or other morphological features and become entrapped the same way by which most insects become prey, as is suggested to occur in other carnivorous plant systems (Williams 1976, Zamora 1995).

A comparison between the arachnid diversity collected through ASP and those collected through CC at each location revealed that sampling the arachnid residents was an adequate, yet not precise, predictor of the arachnids captured. A more accurate predictor of arachnid diversity captured through CC was PT. Moreover, there were large discrepancies between the densities captured in CC and ASP for the agelenids, linyphiids, and many ground arachnids. The funneling web of agelenids and the method may have reduced its chance of being captured. The resident

behavior of the linyphiid subfamilies may have also caused the discrepancy between their densities found through ASP versus CC. Finally, the reduced number of ground arachnids found via ASP may have been due to the sampling method; transient ground arachnids may have been less likely to be found than a sedentary web-residing spider within the short time the plants were checked for arachnids.

Arachnid diversity was more similar between geographically close locations than ones farther away, indicating a geographic effect. In contrast, most CC samples at a location correlated best with the CC samples from other locations when compared across techniques and locations. These data suggest that either: 1) the capture of arachnid fauna by *S. purpurea* is largely independent of the similarity or dissimilarity of arachnid diversity in the environment, or 2) the arachnid fauna was similar across locations. Due to the significant differences in arachnid taxa found between locations, it is likely that *S. purpurea* has a common capture profile regardless of location.

An increase in the clumping of pitchers decreased the rate of prey capture and species richness per pitcher. Therefore, a grouping of pitchers, and therefore morphological features, did not act as a greater attraction to arachnids. This has previously been recorded for interactions between carnivorous plants and insects (Gibson 1983, 1991, Zamora 1995). Using three different carnivorous plant species than the one used in this study (*Sarracenia leucophylla*, *Sarracenia alata*, and *Drosera filiformis tracyi*), Gibson (1983) found that the rate of captured prey per pitcher also followed a negative power curve. Gibson (1983) hypothesized that this phenomenon occurs due to the competition for insect prey between traps of different carnivorous plant species. It is similarly likely that the patterns seen in this study are due to a similar phenomenon: intraspecific competition among *S. purpurea*.

An increase in the clumping of pitchers decreased the rate of residency per pitcher. This phenomenon was most likely due to a limited number of arachnids within a given area. If arachnids are not attracted to pitchers, the residency rate, and therefore the number of webs near

pitcher plants, remains constant. As pitcher density changes due to outside variables, web density remains unchanged, leading to a change in the rate of pitcher residency. In this way, an increase in pitcher clumping leads to a decrease in the rate of arachnid residency.

Although many arachnid taxa were found in similar proportions in the environment, captured by the plant, and as residents of the plant, the propensity of an ecological interaction between arachnids and *S. purpurea* is also directly tied to the sex, maturity, and taxa of arachnid. Moreover, the relationship also depends on the age of the pitchers on the plant, the size of the clump within which the plant is located, and the time of year during which the interaction occurs.

# CHAPTER V

## THE CONSUMPTION OF CARNIVOROUS PLANT NECTAR BY SPIDERS AND HARVESTMEN

### Introduction

Most spiders are generalist predators, feeding upon smaller arthropods (Foelix 1996). However, the diets of these arachnids may also include flower buds (Meehan et al. 2009), pollen (Smith and Mommsen 1984), exuvia (Dondale 1965), dead prey (Knost and Rovner 1975, Riechert and Harp 1987, Sandidge 2003), and plant nectar (Pollard et al. 1995, Jackson et al. 2001, Taylor and Pfannenstiel 2008). Nectivory has also been observed in several families (e.g. Anyphaenidae, Miturgidae, Oxyopidae, Salticidae, and Thomisidae: Pollard et al. 1995, Taylor and Foster 1996, Jackson et al. 2001, Taylor 2004, Taylor and Pfannenstiel 2008). Previously assumed to be a rare phenomenon, it has more recently been hypothesized to be a routine nutrient source for spiders (Jackson et al. 2001).

Experiments confirming nectar consumption by spiders has largely focused on floral nectaries. However, extrafloral nectaries can also be a source of nutrition for spiders (Ruhren and Handel 1999, Whitney 2004, Taylor and Pfannenstiel 2008). Only a few types of extrafloral nectar have been tested for their palatability to spiders. Some of the most prominent, those of carnivorous plants, have never been tested. It is possible that spiders drink carnivorous plant nectar as a source of nutrition.

Carnivorous plants are presumed to use nectar as their main prey retainer / attractant (Schnell 2002, Bennett and Ellison 2009). The most common North American carnivorous plant, the purple pitcher plant, *Sarracenia purpurea*, exudes most of its nectar from the peristome, a structure that forms the "lip" of each pitcher (Adams and Smith 1977, Joel 1986, Juniper et al. 1989, Cipollini et al. 1994). *Sarracenia purpurea* produces more nectar at night than during the

day (Deppe et al. 2000). However, *S. purpurea* produces small amounts of nectar compared to other members of the Sarraceniaceae (Cipollini et al. 1994). The composition of *S. purpurea* nectar differs from commonly tested nectars, notably those of a floral origin, by having greater amounts of sugars and different amino acids (Cipollini et al 1994, Dress et al. 1997, Deppe et al. 2000). Therefore, questions surrounding carnivorous plant nectar and its palatability to spiders are of both composition and quantity.

Most types of nectar have high amounts of carbohydrates and amino acids (Baker et al. 1978, Baker and Baker 1983). Large variations exist in the composition of floral nectar, which largely depends on the type of pollinator (Baker and Baker 1983). In sugar concentration, most nectars range from dilute (~10% sugar) to concentrated (~70% sugar) (Koptur 2005). However, extrafloral nectar, such as that produced by *S. purpurea* pitchers, usually contains a higher sugar concentration than floral nectar (Wunnachit et al. 1992; Koptur 1994). Indeed, the concentration of sucrose and fructose taken from *S. purpurea* extrafloral nectar samples has been shown to be quite high (Juniper et al. 1989, Deppe et al. 2000).

Most types of nectar also contain various additional components such as amino acids. Extrafloral nectar contains higher concentrations of amino acids than floral nectar (Baker et al. 1978). *Sarracenia purpurea* pitcher nectar contains at least nine types of amino acids at various concentrations (Dress et al. 1997).

Many spiders that have not been tested for their propensity to drink nectar are also commonly prey of carnivorous plants. *Sarracenia purpurea* captures a great variety of arachnids (Wray and Brimley 1943, Judd 1959, Heard 1998), many of which belong to the families Linyphiidae and Lycosidae. Like most invertebrates, spiders adjust their diet to fit specific nutritional needs (Mayntz et al. 2005), and therefore, may seek out nectar sources containing high sugar and/or amino acid concentrations for nutritional requirements.

The hypothesis that spiders readily consume *S. purpurea* nectar was tested in several experiments. Harvestmen from the Sclerosomatidae (Leiobunum sp.) and agelenid, lycosid, and

linyphiid spiders were tested for their propensity to drink real and simulated carnivorous plant nectar in both laboratory and field trials.

**Methods**

Agelenid, lycosid, and linyphiid spiders and harvestmen (Sclerosomatidae) were exposed to various nectars and sugar-laden solutions in contact trials to test for their consumption receptivity and duration of consumption. Tested solutions included honey (Gunter's Pure Honey, Berryville, VA), a solution of 60% sucrose and 10% amino acids (MEM Amino Acids solution, Invitrogen Co., Cat. No. 11130-051), and *S. purpurea* nectar.

Spiders and harvestmen were collected at the Blackwater Ecologic Preserve (BEP, 36.87° N, 76.83° W) in eastern Virginia. BEP is a fire-dependent community dominated by turkey oak (*Quercus laevis*) and loblolly pine (*Pinus taeda*), with many herbaceous shrubs and open spaces with low lying plants (Frost and Musselman 1987). Sex and maturity of spiders and harvestmen were determined post-testing.

Each arachnid was tested individually for consumption (yes/no) and the duration of drinking. All arachnids were starved for at least one week prior to exposure to the liquid. Each subject was tested only once. Three replicate tests (each with a different individual) were done for each substance. All trials were conducted in an arena except for those with real *S. purpurea* nectar.

The responses of smaller spiders (Lycosidae and Erigoninae) were tested in a 9 cm diameter x 1.5 cm Petri dish while larger spiders (Agelenidae) and harvestmen were tested in a 30 cm diameter opaque plastic container. During testing, the clear Petri dish was placed in a large cardboard box (30.5 cm x 17.8 cm x 7.6 cm) to minimize outside distractions. Within each container, one cm ring of distilled water was poured around the inside perimeter.

Arachnids were placed in the middle of the container and allowed to contact and drink water if desired. An unmeasured drop of the testing fluid was placed in the center of the

container and the behavior of the arthropods was observed. The following observations were recorded: 1) whether the subject lowered its chelicerae to the tested fluid or not, and 2) if chelicerae were lowered, the time of consumption. Arachnids were observed until they stopped consuming the tested fluid and moved away from it, or if they did not drink the tested fluid, post-contact. Each trial was repeated three times with different individuals.

Testing for *S. purpurea* nectar consumption was done on three different newly emerged pitchers from three different plants. All arachnids were tested for *S. purpurea* consumption except for the agelenids. All tests were done inside the lab on potted plants. Arachnids were placed on a new *S. purpurea* leaf and allowed to crawl over the surface of the leaf until they made contact with the nectar-containing peristome. For tests with *S. purpurea*, arachnids were tested only to see whether or not consumption occurred, not the time of consumption. Observations continued until the subjects stopped consuming nectar and moved away, or if they did not consume nectar, post-contact.

All data were tested for normality and homogeneity of variances prior to analysis. The times of liquid consumption for each spider were transformed (ln transformation). Differences among arachnids in their propensity to drink either honey or the simulated *S. purpurea* nectar were compared using one-factor ANOVAs. The time of consumption of honey and simulated *S. purpurea* nectar among spiders were compared using independent *t*-tests.

**Results**

All arachnids drank the honey provided. The only significant difference among taxa was that the erigonines drank for significantly less time than harvestmen or linyphiines ($F = 8.97$; $df = 3, 25$; $P < 0.001$). Arachnids drank the 60% sucrose + 10% amino acid solution. The only significant difference among taxa was that the linyphiines drank for significantly less time than the lycosids ($F = 5.94$; $df = 3, 16$; $P < 0.01$).

When combined, all spiders and harvestmen drank the honey for a longer period of time

than the 60% sucrose + 10% amino acid solution ($t = 3.14$; df = 56; $P < 0.01$). When tested for the propensity to drink *S. purpurea* nectar, the Erigonines (Fig. 16) and harvestmen (Fig. 17)

FIG. 16. An erigonine consuming nectar of *S. purpurea* from the peristome.

consumed nectar from the peristome, but Linyphiines and Lycosids showed no signs of liquid consumption.

**Discussion**

These results show that spiders and harvestmen consume *S. purpurea* nectar and nectar of a similar composition both in the lab and in the field. Previous studies have shown that spiders may consume extrafloral nectar, but this study presents the first evidence that carnivorous plant nectar is also palatable to spiders and harvestmen.

Extrafloral nectar consumption by spiders has previously been shown in only a few families (Taylor 2004). The observations of nectar consumption in the families Agelenidae,

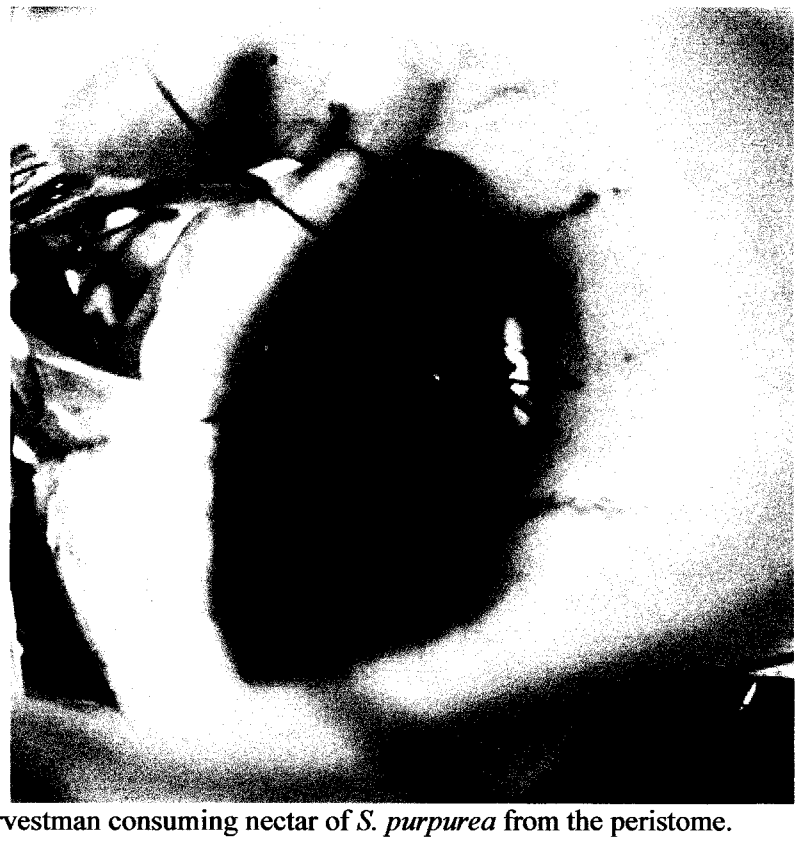

FIG. 17. A harvestman consuming nectar of *S. purpurea* from the peristome.

Lycosidae, Linyphiidae, and in harvestmen are novel. Some wandering or ground spider taxa have been tested for nectar consumption (Anyphaenidae, Miturgidae, Oxyopidae, Salticidae, and Thomisidae). This study shows that spiders of the ground spider taxon, Lycosidae, also consume nectar. Similarly, this is the first study to show that web-building spiders (agelenids and linyphiids) also readily engage in nectar consumption.

The reduced honey-drinking time of the erigonines may have been caused by their smaller size compared to other spiders. Erigonines (adults and spiderlings), were commonly < 3 mm in body length. In contrast, lycosids, linyphiines, and harvestmen were often greater than 1 cm. However, in comparing these taxa in the drinking time of the simulated *S. purpurea* nectar, the Linyphiines drank for the shortest time. Therefore, other unknown compounding factors such as maturity or sex may have played a role in determining consumption time. Similarly, the significantly longer drinking time of honey compared to the simulated *S. purpurea* nectar may

have also been due to these factors.

Although erigonines and harvestmen readily drink *S. purpurea* nectar from the plant, it is unclear why linyphiines or lycosids did not also drink from the peristome. Lycosids are one of the main spider prey of *S. purpurea*, and linyphiines are also common prey. One hypothesis for why these experiments failed to elicit a drinking response in these two groups is that they become prey of *S. purpurea* at night. Night capture of spiders may be tied to two important facts: 1) nectar production by *S. purpurea* increases at night (Deppe et al. 2000), and 2) wandering spiders are most active at night (Foelix 1996, Taylor and Foster 1996). These experiments may have not resulted in *S. purpurea* nectar consumption on the plant because the volume of liquid may not have been enough for these larger tested spiders. These spiders may fall victim to the plant during the night, when nectar levels are high, therefore resulting in high capture densities. Further studies into the diel variation in nectar concentration and the periodicity in prey capture by *S. purpurea* may yield further insights into this phenomenon.

Spiders and harvestmen are common prey of carnivorous plants, but this status has remained an enigma since it was not known why they would visit carnivorous plants. These results show that carnivorous plant nectar can be a reward for spiders and harvestmen just as it is for insects. Subsequently, their capture by *S. purpurea* may occur through the same mechanism by which insects are captured – through slips and falls into the pitcher (Schnell 2002).

# CHAPTER VI

## SPIDER / HARVESTMAN AND INSECT DENSITY IN RELATION TO THE MORPHOLOGICAL FEATURES OF *SARRACENIA PURPUREA*

### Introduction

The capture of prey by *S. purpurea* has been hypothesized to involve three separate phenomena: their attraction, retention, and capture (Juniper et al. 1989). There is conflicting evidence concerning the role of morphological features in prey capture by *S. purpurea*. Like other carnivorous plants, nectar has been presumed to be a prey lure (Joel 1986, Schnell 2002) and experiments have demonstrated high capture using only a nectar source (Bennett and Ellison 2009). Similarly, red pigment is positively associated with prey visitation (Newell and Nastase 1998) and capture (Fish and Hall 1978, Cresswell 1991). Furthermore, younger and larger pitchers have increased rates of prey capture (Fish and Hall 1978, Wolfe 1981, Cresswell 1993, Green and Horner 2007), presumably due to an enhancement of morphological features.

Many of the morphological features that are assumed to be active attractants (i.e. luring of prey), may actually merely increase the ability of the plant to retain randomly visiting prey (Juniper et al. 1989). This hypothesis is supported by the fact that the frequency of visits by potential prey is not associated with pitcher age or size, temperature, or time of day (Newell and Nastase 1998). Moreover, potential prey visit carnivorous plants and the surrounding vegetation at equal frequencies (Williams 1976, Zamora 1995). Furthermore, the hypothesis of red pigment as an attractant is jeopardized by observations that plants without pigment are as equally successful at prey capture as pigmented ones (Sheridan et al. 2000, Green and Horner 2007).

*Sarracenia purpurea* produces nectar from glands located on the exterior of the pitcher (Russell 1919, Joel 1986, Juniper et al. 1989), but mostly from the lip/nectar roll (peristome) (Adams and Smith 1977, Joel 1986, Juniper et al. 1989, Cipollini et al. 1994). A similar form, *S.*

*purpurea purpurea* f. *heterophylla*, lacks pigment but produces nectar. This form exists in small pockets of wetlands that occur from Massachusetts and Newfoundland westward to Minnesota (Schnell 2002).

Carnivorous plant models placed alongside live plants have been used to test the efficacy of morphological features (Zamora 1990, 1995, Bhattarai and Horner 2009, Bennett and Ellison 2009), pattern of insect capture (Karlsson et al. 1987, Zamora 1990, 1995, Bhattarai and Horner 2009), pitcher water balance (Kingsolver 1981), community dynamics (Heard 1994a, Cochran-Stafira and von Ende 1998), and site-selection by phytotelmatous (leaf-water inhabiting) organisms (Ratsirarson and Silander 1996). Models of pitcher plants enable controlled comparisons with live plants while excluding nectar and pigment. In the present study, model pitchers were filled with water but lacked nectar and pigment.

Spiders are often captured by pitcher plants (Wray and Brimley 1943, Judd 1959, Heard 1998), occasionally use the pitchers as oviposition sites (Rymal and Folkerts 1982; Milne *unpublished data*), and may take up residence on pitchers (Cresswell 1991). Most spiders capture prey either by building webs or sit-and-wait predation (Foelix 1996). Spiders choose habitats for residency based on a variety of factors, including the abundance of prey (Martyniuk 1983, Harwood et al. 2001, Harwood et al. 2003), vegetation structure (Lowrie 1948, Greenstone 1984, De Omena and Romero 2008), temperature, and humidity (Rypstra 1986, Gillespie 1987, Wise 1993). Web-building spiders frequently select locations with high prey densities (Martyniuk 1983, Rypstra 1985, Harwood et al. 2001). Interactions between spiders and carnivorous plants have been noted (Hubbard 1896, Sudman 1999, Anderson and Midgley 2002) but arachnid response to the morphological features of carnivorous plants has only been studied for the linyphiids (Cresswell 1993).

In the present study the random placement of plants and models were used in field trials to test the hypothesis that arthropod capture and arachnid residency are affected by the presence of nectar, pigment, and pitcher water with decomposing prey. The effect of pitcher age on

capture success was assessed by the simultaneous sampling of new and old pitchers. A secondary goal was to correlate the rates of arachnid capture and residency to the rates of prey capture, pitcher age, and pitcher size.

**Methods**

In eastern Virginia, the 319 acre Blackwater Ecologic Preserve (BEP, 36.87° N, 76.83° W) is a fire-dependent community dominated by turkey oak (*Quercus laevis*) and loblolly pine (*Pinus taeda*), with many herbaceous shrubs and open spaces with low lying plants (Frost and Musselman 1987). Different areas of the preserve are subjected to prescribed burns at least once a year. Approximately 15 – 25 naturally occurring clumps of *S. purpurea* occur there.

Five different pitcher plant-like treatments were used in this study: *S. purpurea venosa* with no manipulation (containing nectar, pigment, and water; henceforth 'N+P+W+'), *S. purpurea purpurea* f. *heterophylla* with no manipulation (containing nectar and water; henceforth 'N+P-W+'), *S. purpurea venosa* with pitchers 3/4 filled with cotton balls (containing nectar and pigment; henceforth 'N+P+W-'; used in arachnid residency studies but not used in capture studies), *S. purpurea venosa* with nectar glands covered along the lip (peristome) of the pitchers (containing pigment and water; henceforth 'N-P+W+'), and blue polyurethane *S. purpurea* models (containing only water; henceforth 'N-P-W+'). Five replicates of each of these treatments (twenty-five, total) were created. Plants were clipped so that each had five pitchers and models were made with five pitchers.

Each N-P+W+ had its peristome covered with a clear, quick-hardening sealant (Lexel super-elastic sealant, Sashco Sealants, Inc.). In a preliminary study, slices approximately 1 mm thick were cut from the peristome of sealed pitchers and mounted on a slide. Examination of slides under light microscopy at 20x revealed that this sealant covered the stomata on the epidermal surface (Fig. 18) and therefore plugged any other glands associated with nectar production. This was also evidenced by observations of decaying peristome tissue of N-P+W+

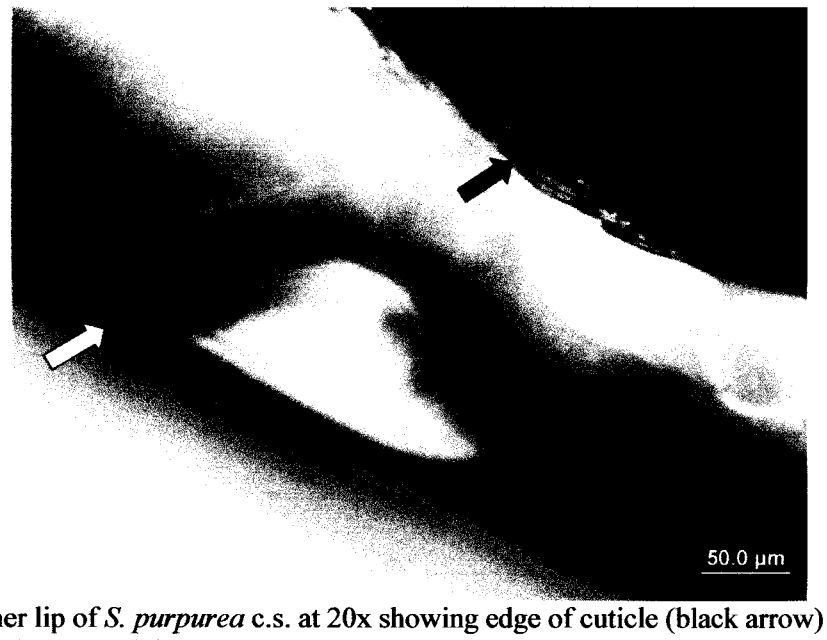


FIG. 18. Pitcher lip of *S. purpurea* c.s. at 20x showing edge of cuticle (black arrow) covered by sealant (s) and the edge of the sealant (white arrow).

pitchers.

All plants were grown in a pre-moistened Canadian sphagnum peat and locally harvested silica masonry sand mixture (Caroline County, VA) in a 50:50 ratio at the Meadowview Biological Research Station in Woodford, VA. Plants were maintained outdoors under ambient conditions in full sun at Meadowview in water tanks at 1/3 the pot height. The water source was a local tannic, dystrophic pond. All plants had their contents removed and were trimmed to five pitchers at the time of planting.

Models were created from metal core-boxes and molds shaped like *S. purpurea* pitchers. Wax (Gulf Paraffin Wax, Royal Oak Enterprises, Inc.) cores were created with the metal core-boxes and were used to create the insides of pitchers. The wax cores were placed inside the plaster molds and liquid polyurethane was poured around the wax to create the outside of pitchers. After the polyurethane hardened, the inner wax was melted and removed, creating a hollow pitcher. Five of these pitchers were then set up in a rosette and sealed together at the base with a ring of polyurethane (Fig. 19).

FIG. 19. Polyurethane model of pitcher plant.

A 100 m x 100 m (1000 $m^2$) area was selected for plant placement that was adjacent to naturally growing pitcher plants and vegetation similar to areas at BEP where natural populations of *S. purpurea* grew. This area was partitioned using a 1 m grid system. X and y coordinates for points of plant placement in the grid were selected through the use of a random number generator (Haahr 2007). All plants were kept in pots (16.5cm diameter x 18.4cm depth) and placed into the soil so that the top of the pot was flush with the ground (Fig. 20). Leaf litter from adjacent areas was spread at the base of the plants and the plant models so that it resembled the surrounding area. Manipulations to the plants to create the different treatments were conducted on the first day of setup once they were planted. All plants and models were watered every day of data collection.

Treatments were set in the field on April 28$^{th}$, 2008, and were allowed to equilibrate in the surrounding area for one week prior to data collection. After this time, contents of all plants and models were removed and discarded. Pitchers were filled half-full with distilled water. Prey captured by all plants and models were removed with turkey basters and smaller plastic pipettes

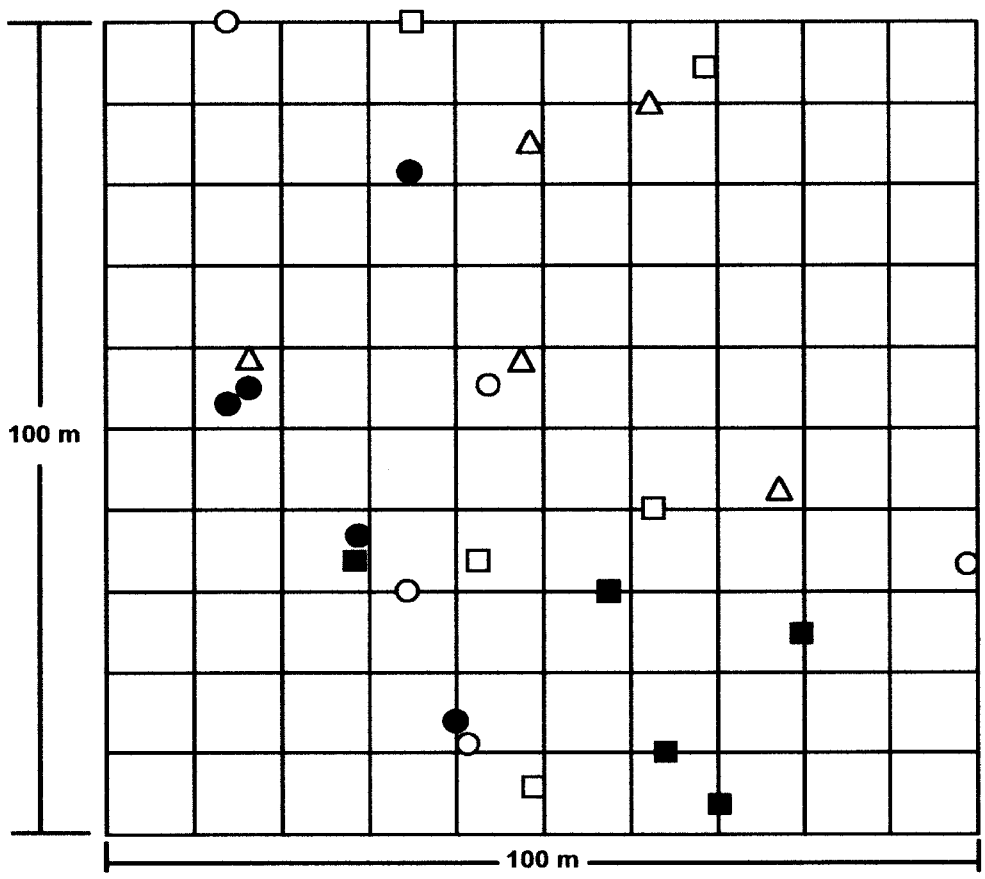


FIG. 20. Experimental layout at BEP within a 1000 $m^2$ area. Filled square = N+P+W-, Filled circle = N+P+W+, Open square = N-P+W+, Open triangle = N+P-W+, Open circle = N-P-W+.

and preserved once a week for nine weeks. Pitchers were refilled with distilled water and left to collect prey for another week. Arachnids found walking on, inhabiting a web directly over (< 5 cm), or inhabiting a web inside the pitchers of plants and models (i.e. resident arachnids) were also removed three times a week for four weeks and then once a week for a month afterwards. The position (web over pitcher, web inside pitcher, web against pitcher, or walking on plant) of residing arachnids was recorded, after which they were collected and preserved for later identification. Plant-captured and resident adult arachnids were identified to species using Ubick et al. (2005) and insects were identified to order (Triplehorn and Johnson 2005).

Pitcher development was tracked over the course of the experiment so that new and old pitchers could be compared to arachnid capture rate. Once a new pitcher opened, the date was

marked with a permanent marker on the outside of the hood and the most senesced pitcher on the plant was removed in order to maintain five on each plant. The size of the pitcher opening (pitcher size) was also measured. This measurement consisted of the width of the pitcher peristome. Manipulations to pitchers were conducted on the earliest date new pitchers opened.

Data were tested for homogeneity of variances and normality prior to statistical analyses; if data did not fit these parameters, they were transformed. Differences between the total number of female and male, mature and spiderling, or ground and web-building arachnids captured or residents were each separately analyzed via an independent samples *t*-test. Differences among treatments were done via MANOVA with a Tukey's HSD multiple comparisons test.

Capture efficiency (both arachnids captured/pitcher and non-arachnids captured/pitcher) for new, old, and total pitchers among treatments (model pitchers were treated as "old" due to similar performance in capture efficiency) were compared with a one-factor ANOVA with a Tukey's HSD post-hoc multiple comparisons test. The diversity of prey caught in each treatment type was determined using the Shannon-Weiner Diversity Index. The diversity of arachnids, non-arachnids, and total prey among treatments were analyzed via a MANOVA with a Tukey's HSD post-hoc multiple comparisons test. A three-way ANOVA with a Tukey's HSD multiple comparisons was used to test between the number of prey caught between new and old pitchers in each treatment type for each order.

Null models of prey capture were created by using the proportion of pitchers on each plant that were new over time as x and y data coordinates where the x-axis is the proportion of new pitchers and the y-axis is the proportion of arachnids visiting new pitchers. Independent *t*-tests were used to determine statistical difference between the slope of the null model and that of either insect capture or arachnid capture for each treatment type. A Bonferonni correction was used to control for multiple *t*-tests, reducing the *P*-value for significance to 0.008.

Pearson's correlations were used to compare the density of captured arachnids and non-arachnids, captured arachnids and resident arachnids, arachnid residents and captured non-

arachnids, and pitcher opening size and captured insect and arachnid densities. An independent samples *t*-test was also used to compare the total number of resident linyphiines to the total number of captured linyphiines over all treatments - the same type of test was used to test for differences between residents and captured erigonines.

Specialization by all pitcher plants and by each treatment type was determined using the probability of an interspecific encounter (PIE) analysis (Hurlbert 1971). PIE ranges from 0 – 1 and was used here to measure the degree that each treatment type specialized on any one specific prey item. An ANOVA was used to compare PIE among treatments.

**Results**

Plants and models captured 11 orders of insects, Coleoptera, Collembola, Diptera, Hemiptera, Hymenoptera, Isoptera, Lepidoptera, Neuroptera, Orthoptera, Psocoptera, and Thysanoptera (Table 12). In addition, snails, slugs, and arachnids were also captured.

TABLE 12. Mean number ± SE of prey captured by all treatments. N = 9 except for Grand Mean. H = Hymenoptera, C = Collembola, A = Acari, D = Diptera, T = Thysanoptera, Co = Coleoptera, Ar = Araneae, P = Psocoptera, O = Other (Hemiptera, Orthoptera, Lepidoptera, Mollusca, Isoptera, and Neuroptera)

| Treatment | H | C | A | D | T | Co | Ar | P | O |
|---|---|---|---|---|---|---|---|---|---|
| N+P-W+ | 667.6 | 346.4 | 59.0 | 32.8 | 34.4 | 13.6 | 17.6 | 23.6 | 10.0 |
| SE | 338.5 | 126.1 | 4.7 | 10.1 | 19.3 | 3.7 | 5.2 | 23.6 | 2.5 |
| N-P+W+ | 756.4 | 229.6 | 60.6 | 23.0 | 20.2 | 16.0 | 16.8 | 2.4 | 6.8 |
| SE | 238.7 | 39.1 | 17.5 | 6.4 | 16.8 | 9.3 | 1.9 | 0.7 | 2.5 |
| N+P+W+ | 605.8 | 444.8 | 249.6 | 20.6 | 5.2 | 22.0 | 20.2 | 19.0 | 10.2 |
| SE | 476.7 | 137.3 | 160.7 | 8.0 | 1.7 | 7.0 | 4.9 | 17.5 | 4.3 |
| N-P-W+ | 20.2 | 35.0 | 56.8 | 1.0 | 1.2 | 6.0 | 2.2 | 3.2 | 1.4 |
| SE | 8.8 | 9.8 | 16.9 | 0.6 | 0.6 | 2.4 | 0.4 | 1.7 | 0.7 |
| Grand Mean | 512.5 | 264.0 | 106.5 | 19.4 | 15.3 | 14.4 | 14.2 | 12.1 | 7.1 |

Hymenopterans, mostly ants, were the most common prey captured by all combined treatments.

Twelve families of spiders and one family of harvestmen were found within the treatments. The most common spider species captured were *Shizocosa duplex* (Lycosidae - 28), *Pardosa saxatilis* (Lycosidae - 21), and *Ceratinopsis interpres* (Linyphiidae - 16). Lycosids were the most common arachnid taxon collected over all treatments. Ground arachnids were more often found than web-building arachnids in all living treatments ($t = 2.90$; df = 38; $P = 0.006$). A MANOVA revealed that web arachnids were more often caught in N+P-W+ than N-P-W+ ($F = 11.31$; df = 3, 16; Tukey's HSD: $P = 0.002$ and $P = 0.025$, respectively). In addition, all treatments caught more ground arachnids than the model (MANOVA, $F = 4.13$; df = 3, 16; Tukey's HSD: N+P+W+: $P < 0.001$; N+P-W+: $P = 0.002$; N-P+W+: $P < 0.001$).

There was no significant difference in the number of non-arachnid prey ($F = 1.51$; df = 3, 16; $P = 0.251$) or arachnid prey ($F = 2.83$; df = 3, 16; $P = 0.072$) caught by old and model pitchers among all treatments (Fig. 21). However, models captured significantly fewer arachnid ($F_{3, 16} = 8.07$; df = 3, 16; $P = 0.002$) and non-arachnid ($F = 23.9$; df = 3, 16; $P < 0.001$) prey compared to the total number of each type of prey caught by other treatments when new and old

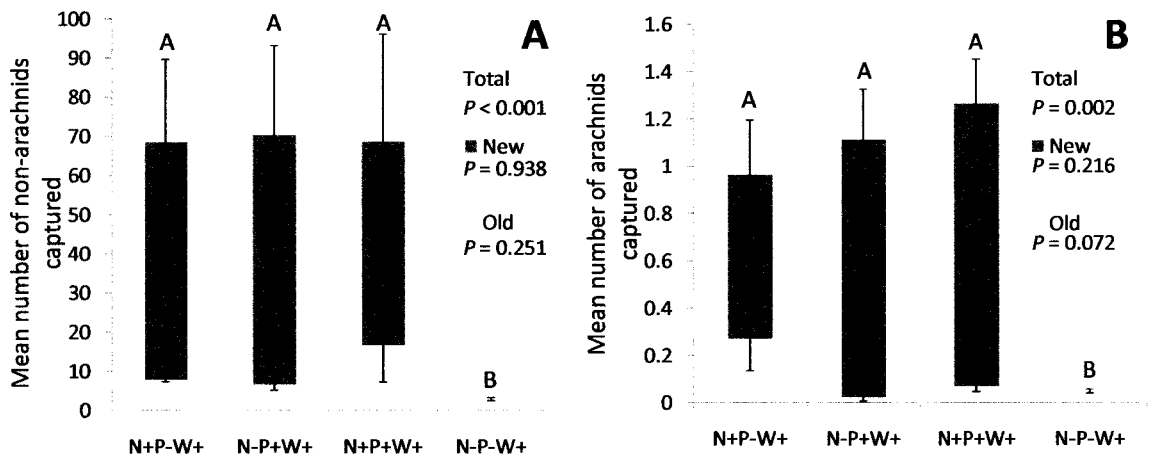


FIG. 21. Numbers and diversities of captured arachnids and non-arachnids. (A) Mean + SE density of non-arachnids captured in new and old pitchers per treatment type; (B) Mean + SE density of arachnids captured in new and old pitchers per treatment type. Different letters indicate significant statistical differences at $P = 0.05$ for total prey captured.

pitcher captures were combined (Fig. 21). There was also no significant difference in the number of non-arachnid prey ($F = 0.07$; df = 2, 12; $P = 0.938$) or arachnid prey ($F = 1.75$; df = 2, 12; $P = 0.216$) captured by new pitchers among the living treatments (Fig. 21).

No significant difference was found in the Shannon-Weiner diversity of non-arachnids (MANOVA, $F = 1.16$; df = 3, 16; $P = 0.354$) or total organisms (MANOVA, $F = 0.991$; df = 3, 16; $P = 0.422$) caught by all pitchers in each treatment type (Fig. 22). However, N-P-W+ caught a significantly less diverse arachnid fauna than any of the other three actively catching treatments (MANOVA, $F = 11.71$; df = 3, 16; $P < 0.001$) (Fig. 22).

A three-way ANOVA of rank-transformed data revealed significant differences among orders ($F = 74.03$; df = 10, 264; $P < 0.001$), treatments ($F = 3.05$; df = 2, 264; $P = 0.049$), and

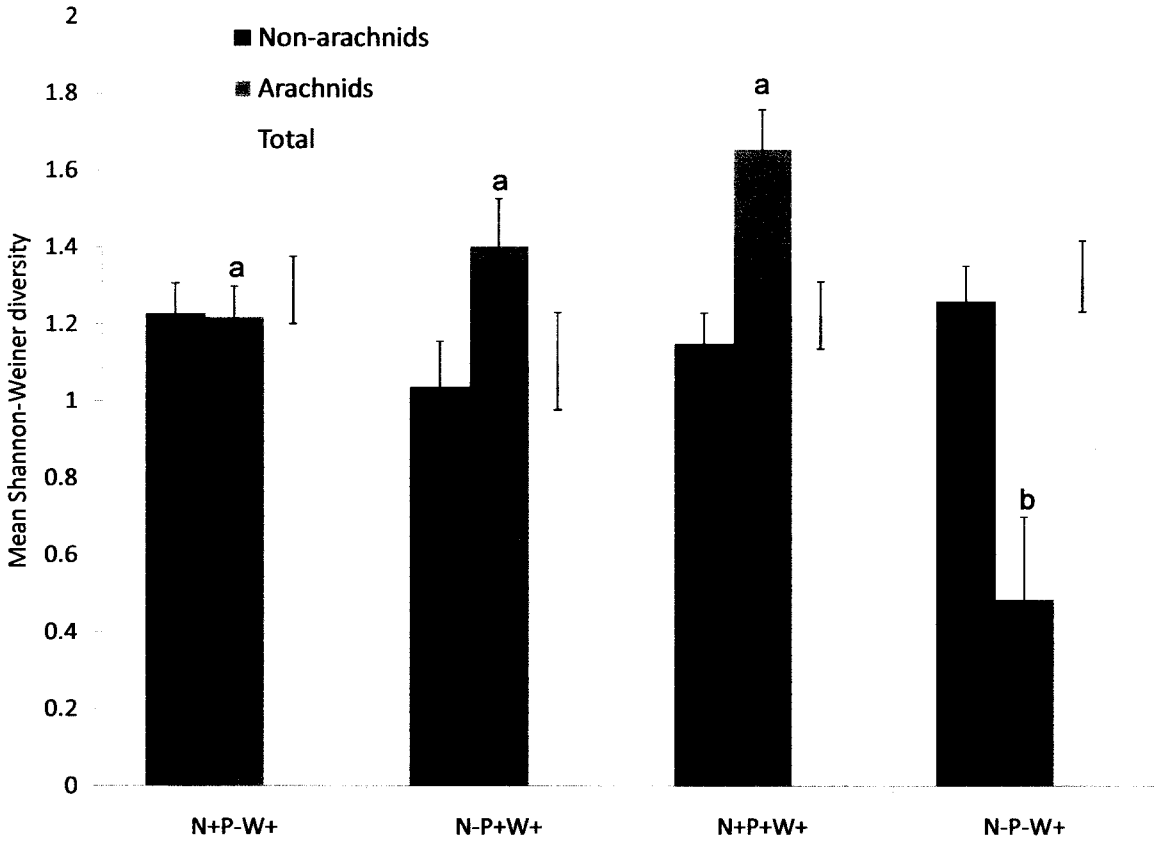


FIG. 22. Mean + SE Shannon-Weiner diversity index of arachnid, non-arachnid, and total captured prey per treatment type. Different letters of the same subscript indicate statistical differences among treatments at $P = 0.05$.

pitcher age ($F = 158.7$; df = 1, 264; $P < 0.001$). Of all four interactions, only the order * age interaction was significant ($F = 7.69$; df = 10, 264; $P < 0.001$). A follow up Tukey post-hoc test on the order * age interaction revealed that Hymenoptera ($P < 0.001$), Hemiptera ($P = 0.001$), Diptera ($P < 0.001$), Coleoptera ($P < 0.001$), Thysanoptera ($P < 0.001$), Orthoptera ($P = 0.008$), and Araneae ($P < 0.001$) were significantly more often captured by new pitchers while there was no significant difference in the capture of Collembola ($P = 1.0$), Acari ($P = 1.0$), Psocoptera ($P = 0.729$), and other prey (Neuroptera, Isoptera, Lepidoptera, Mollusca, and unknown prey; $P = 1.0$) between new and old pitchers (Table 13).

TABLE 13. Mean ± SE number of prey per new and old pitchers for all taxa and the statistical difference between them (Tukey test, *P*-value). "Other" = Neuroptera, Isoptera, Lepidoptera, and Mullosca.

| | Mean ± SE | | | | |
|---|---|---|---|---|---|
| | New | SE | Old | SE | *P* |
| Collembola | 13.11 | 2.82 | 5.03 | 1.07 | 1 |
| Hymenoptera | 39.99 | 10.29 | 1.06 | 0.15 | < 0.001 |
| Acari | 1.43 | 0.19 | 3.85 | 2.19 | 1 |
| Hemiptera | 0.24 | 0.04 | 0.04 | 0.01 | 0.001 |
| Diptera | 1.25 | 0.18 | 0.13 | 0.02 | < 0.001 |
| Psocoptera | 0.64 | 0.39 | 0.07 | 0.05 | 0.729 |
| Coleoptera | 0.87 | 0.18 | 0.09 | 0.02 | < 0.001 |
| Thysanoptera | 1.01 | 0.35 | 0.03 | 0.01 | < 0.001 |
| Orthoptera | 0.18 | 0.06 | 0.01 | 0.00 | 0.008 |
| Other | 0.05 | 0.01 | 0.06 | 0.02 | 1 |
| Araneae | 1.00 | 0.13 | 0.12 | 0.05 | < 0.001 |

There was no significant difference among treatments in the PIE of prey items ($F = 1.21$; df = 3, 19; $P = 0.338$). However, even though the overall specialization of each treatment type was non-significant, the taxon on which N-P-W+ specialized the most (Acari) differed from that which the other three treatments specialized (Hymenoptera) (Fig. 23).

All three plant treatments (N+P+W+, N+P-W+, and N-P+W+) caught significantly more

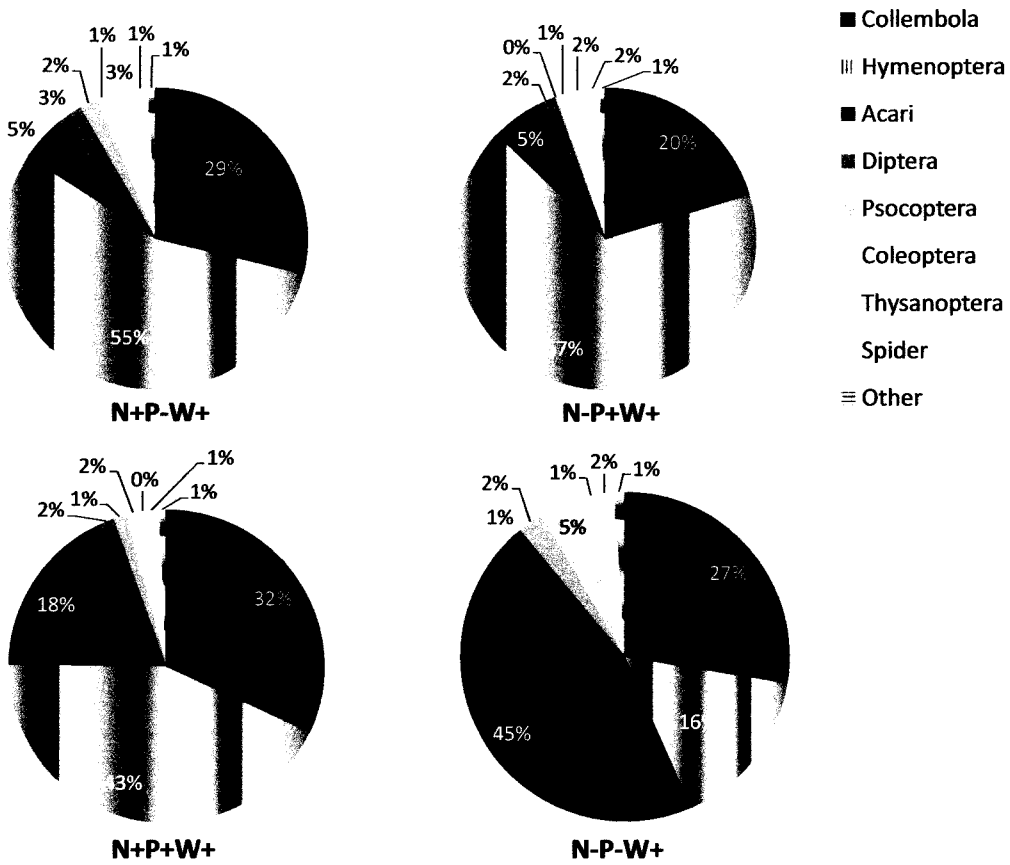


FIG. 23. Relative composition of prey for each treatment type. "Other" includes Hemiptera, Neuroptera, Isoptera, Orthoptera, Lepidoptera, and Mollusca.

arachnid and non-arachnid prey in new pitchers than what was expected by the null model, which predicted that the proportion of new pitchers should equal the proportion of arachnids captured in those new pitchers (N+P+W+: $t = 4.06$; df = 1; $P < 0.01$ (non-arachnid prey), $t = 3.37$; df = 1; $P < 0.01$ (arachnid prey); N+P-W+: $t = 4.99$; df = 1; $P < 0.001$ (non-arachnid prey), $t = 3.81$; df = 1; $P < 0.01$ (arachnid prey); and N-P+W+: $t = 5.28$; df = 1; $P < 0.001$ (non-arachnid prey), $t = 3.25$; df = 1; $P < 0.01$ (arachnid prey)) (Fig. 24).

Pitcher size was significantly negatively correlated to captured insect density due to the inclusion of low-capturing, large pitcher, model data ($r^2 = 0.208$; $P = 0.043$; $n = 20$). When the model data were removed, the data were non-significant ($r^2 = 0.0016$; $P = 0.888$; $n = 15$). Pitcher size similarly affected arachnid capture; a significant negative correlation was present when

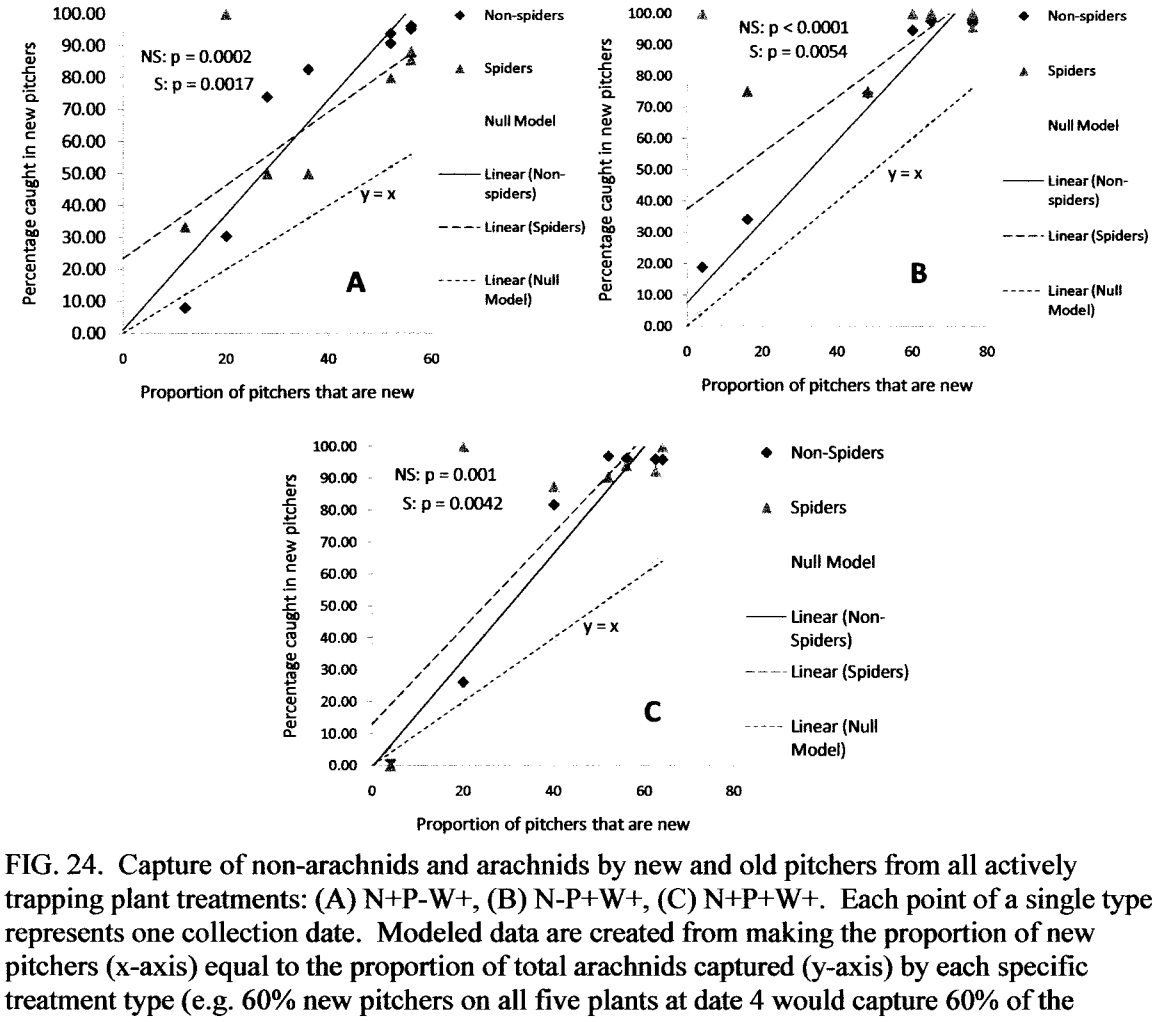


FIG. 24. Capture of non-arachnids and arachnids by new and old pitchers from all actively trapping plant treatments: (A) N+P-W+, (B) N-P+W+, (C) N+P+W+. Each point of a single type represents one collection date. Modeled data are created from making the proportion of new pitchers (x-axis) equal to the proportion of total arachnids captured (y-axis) by each specific treatment type (e.g. 60% new pitchers on all five plants at date 4 would capture 60% of the arachnids caught by that treatment on that date). For the null model, y = x.

model data were included ($r^2 = 0.489$; $P = 0.001$; $n = 20$) but non-significant when model data were removed ($r^2 = 0.070$; $P = 0.339$; $n = 15$). There was no correlation between pitcher size and the number of arachnid residents present when model data were included ($r^2 = 0.034$; $P = 0.435$; $n = 20$) or excluded ($r^2 = 0.070$; $P = 0.339$; $n = 15$).

There was no correlation between the density of non-arachnid prey captured and the density of arachnid residents found on all treatment types ($r^2 = 0.049$; $P = 0.347$; $n = 20$) (Fig. 25a). There was a strong correlation between the density of arachnids captured and the density of non-arachnids captured over all treatment types ($r^2 = 0.697$; $P < 0.0001$; $n = 20$) (Fig. 25b).

Finally, there was no significant correlation between the density of arachnid residents and arachnid prey found on all treatment types ($r^2 = 0.166$; $P = 0.074$; $n = 20$) (Fig. 25c).

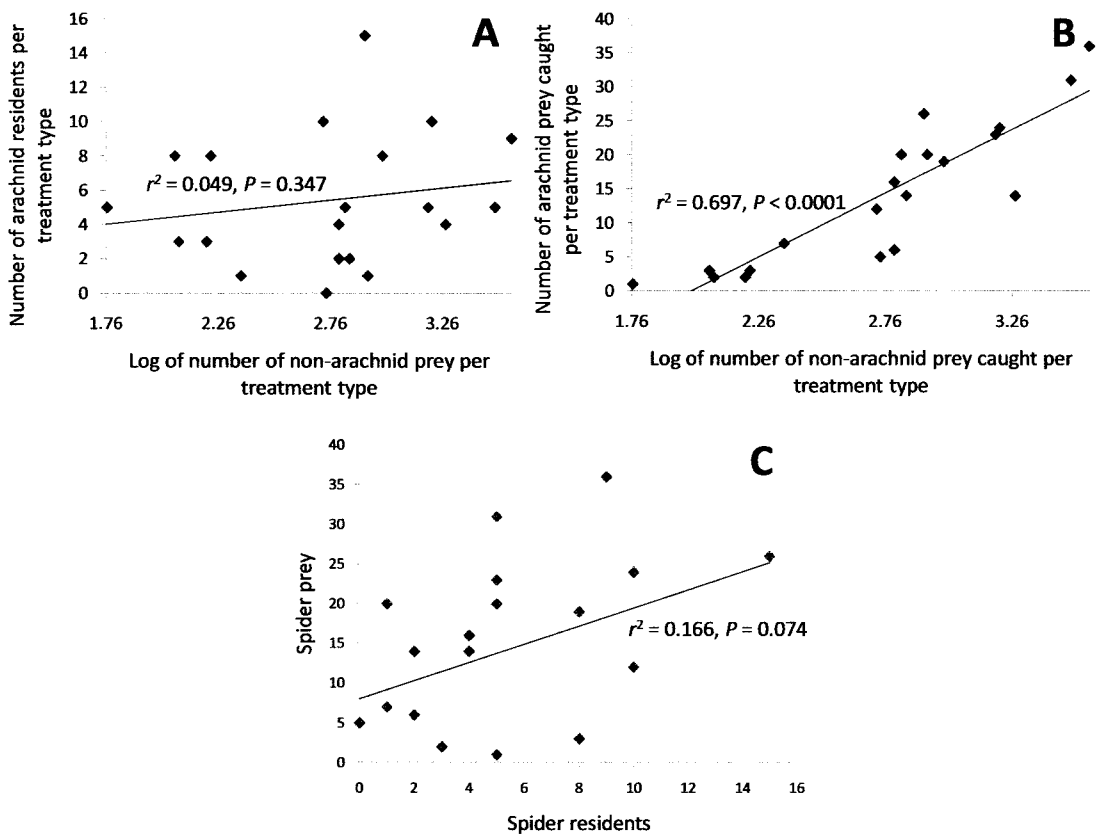


FIG. 25. Various correlations between arachnid prey and residents. Each point represents one plant. (A) Correlation between the number of arachnid residents and the number of non-arachnid prey found on all treatments; (B) Correlation between the number of arachnid prey and non-arachnid prey caught by all treatments; (C) Correlation between the number of arachnid prey caught by all treatments and the number of arachnid residents found on all treatments

Although there was no statistical difference between the total number of male and female arachnids caught over all combined treatments ($t = 1.41$; df = 38; $P = 0.166$), N+P+W+ captured a significantly greater number of females than N+P-W+ (MANOVA, $F < 0.001$; df = 3, 16; $P = 0.002$). N+P+W+ and N-P+W+ caught a significantly greater number of females than N-P-W+ (Tukey's HSD: $P = 0.003$ and $P < 0.001$, respectively). Both N+P-W+ and N-P+W+ caught a significantly greater number of males than the model (MANOVA, $F = 4.43$; df = 3, 16; Tukey's

HSD: $P = 0.046$, $P = 0.019$, respectively); treatments showed trends of male capture (Fig. 26a).

There was no statistical difference between the total number of adult and immature arachnids caught over all combined treatments ($t = 1.13$; df = 38; $P = 0.264$), yet most treatments tended to catch more adults (Fig. 26b). Among treatments, a MANOVA revealed that N+P-W+,

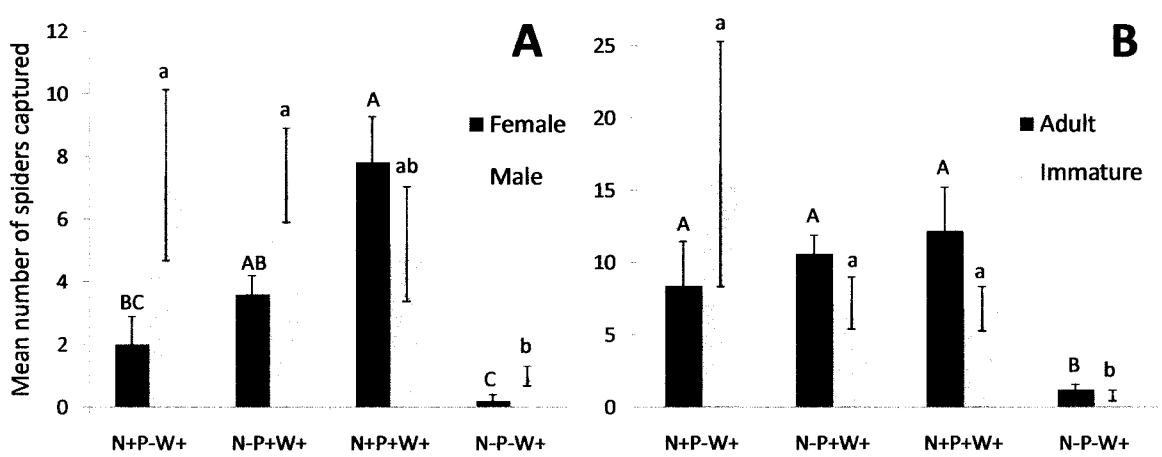


FIG. 26. (A) Mean ± SE number female and male arachnids caught per treatment type; (B) Mean ± SE number of mature and immature arachnids caught per treatment type. Different letters indicate statistical differences among treatments at $P = 0.05$.

N-P+W+, and N+P+W+ all caught more adults than N-P-W+ ($F_{3, 16} = 8.46$; df = 3, 16; Tukey's HSD: $P = 0.049$, $P = 0.002$, $P = 0.004$, respectively). A similar pattern was revealed with immatures in that N+P-W+, N-P+W+, and N+P+W+ all caught more immatures than N-P-W+ (MANOVA, $F = 6.36$; df = 3, 16; Tukey's HSD: $P = 0.006$, $P = 0.017$, $P = 0.025$, respectively).

Individuals of eight families of spiders and one family of harvestmen were found residing over or crawling on all treatments. The most common residents were *Agyneta* sp. 1 (16), *Ceratinopsis interpres* (12), and *Agyneta* sp. 2 (7), all of which are members of the sheet-web weaving family Linyphiidae. Members of the subfamily Linyphiinae (family Linyphiidae) were the most common arachnid taxa found residing over all treatments. Although there was no difference in the total density of residents that was found on each treatment type (MANOVA, $F =$ 0.498, df = 4, 20; $P = 0.738$) (Fig. 27), over all treatments, resident web-building arachnids were

found significantly more often than resident ground spiders ($t = 4.07$; df = 48; $P < 0.001$) (Fig. 28). However, there was no difference among treatments in the number of ground (MANOVA, $F = 0.442$; df = 4, 20; $P = 0.777$) or web-building spider residents (MANOVA, $F = 0.332$; df = 4, 20; $P = 0.853$) (Fig. 27).

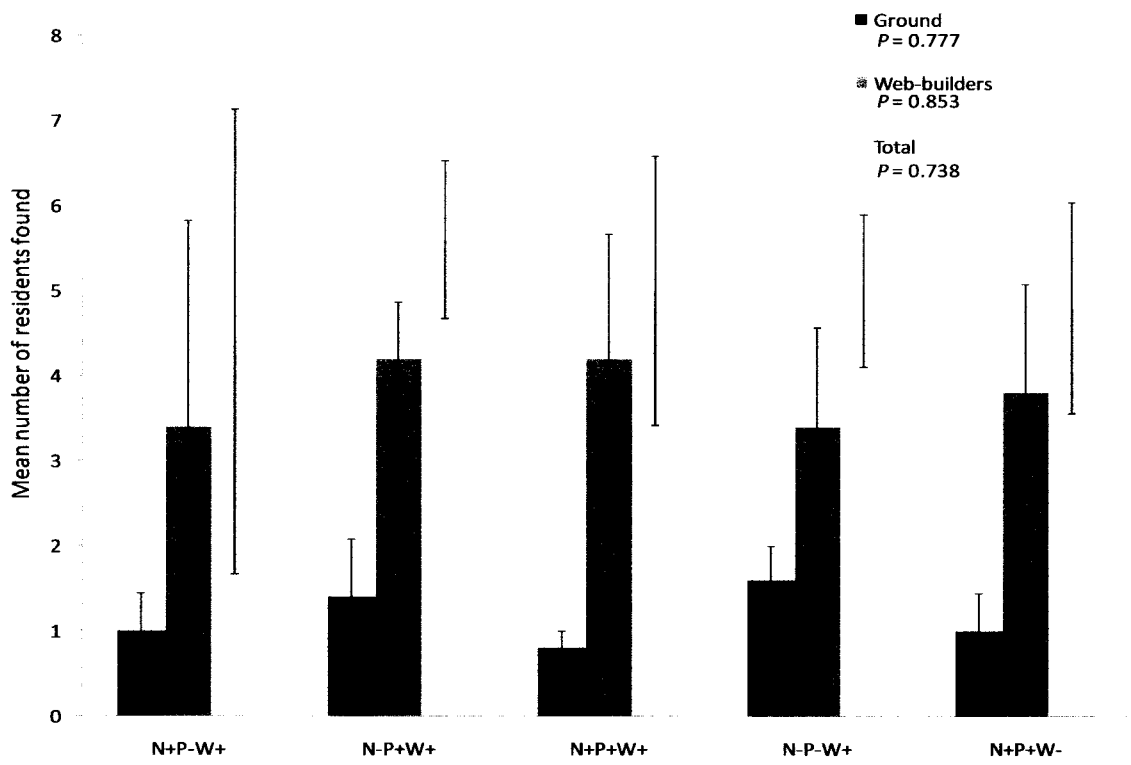


FIG. 27. Mean ± SE density of ground, web-building, and total arachnid residents per treatment type.

There was no significant difference over all treatments between the number of female and male arachnid residents found ($t = 1.02$; df = 48; $P = 0.314$). There was also no significant difference among treatments in the number of female (MANOVA, $F = 0.775$; df = 4, 20; $P = 0.555$) or male residents found (MANOVA, $F = 0.850$, df = 4, 20; $P = 0.511$) (Fig. 29).

There was no significant difference over all treatments between the number of adult and immature arachnid residents found ($t = 0.161$; df = 48; $P = 0.873$). There was also no significant difference among treatments in the number of mature (MANOVA, $F = 1.15$; df = 4, 20; $P =$

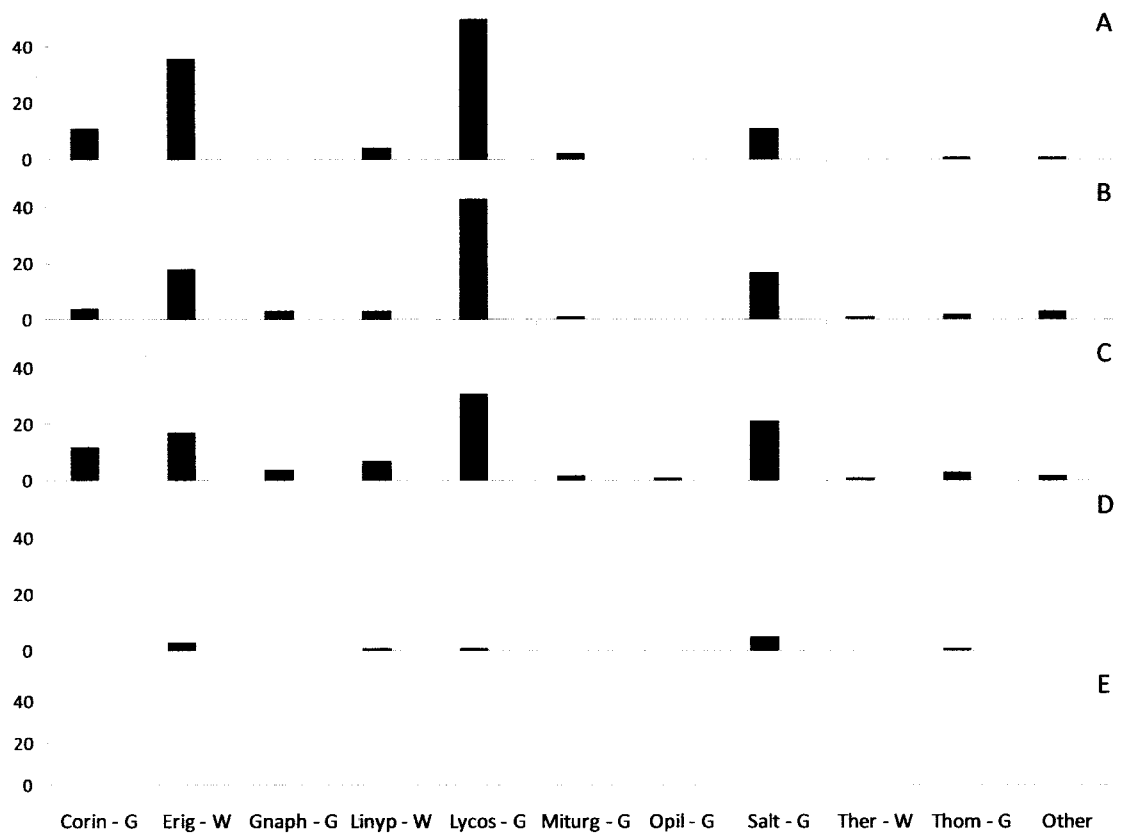


FIG. 28. Total number of arachnid prey and residents of various treatments. Black bars represent numbers of prey captured and grey bars represent number of residents found. (A) N+P-W+; (B) N-P+W+; (C) N+P+W+; (D) N-P-W+; (E) N+P+W-. Corin = Corinnidae, Erig = Erigoninae, Gnaph = Gnaphosidae, Linyp = Linyphiinae, Lycos = Lycosidae, Miturg = Miturgidae, Opil = Opiliones, Salt = Salticidae, Ther = Theridiidae, Thom = Thomisidae. "Other" includes the families Agelenidae, Araneidae, Dictynidae, Oxyopidae, Philodromidae, and Tetragnathidae. "G" after the family abbreviation designates a primarily ground arachnid family and "W" after the family abbreviation designates a primarily web-building arachnid family.

0.362) or immature residents found (MANOVA, $F = 0.081$; df = 4, 20; $P = 0.987$) (Fig. 29).

Linyphiid spiders were the most prevalent web-builders near all treatments. Spiders of this taxa accounted for 83.5% of the diversity in webs near the plant. These spiders were three times as abundant as residents as erigonines. Although linyphiine spiderlings accounted for 38% of the total resident linyphiines, they made up 60% of the captured linyphiines. A similar pattern was found for erigonines whereby the spiderlings accounted for 30% of total resident erigonines and made up 55% of the captured erigonines. However, there was no difference between the proportion of mature and immature erigonines found in webs over, in, or against pitchers (Fig.

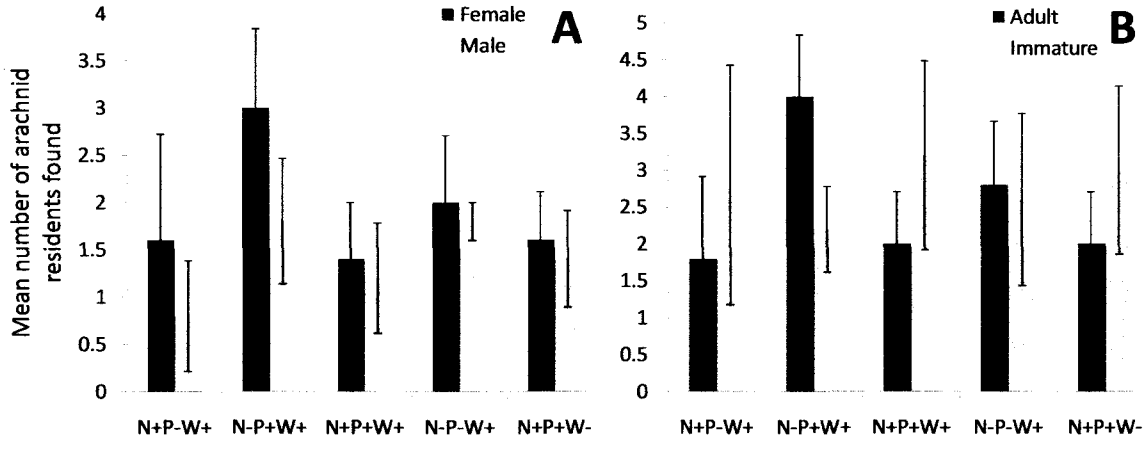


FIG. 29. (A) Mean ± SE number of female and male resident arachnids near pitchers per treatment type; (B) Mean ± SE number of mature and immature resident arachnids near pitchers per treatment type.

30). There was a significantly greater number of linyphiines found residing over treatments than captured in treatments ($t = 3.10$; df = 43; $P = 0.003$) and there was a significantly greater number

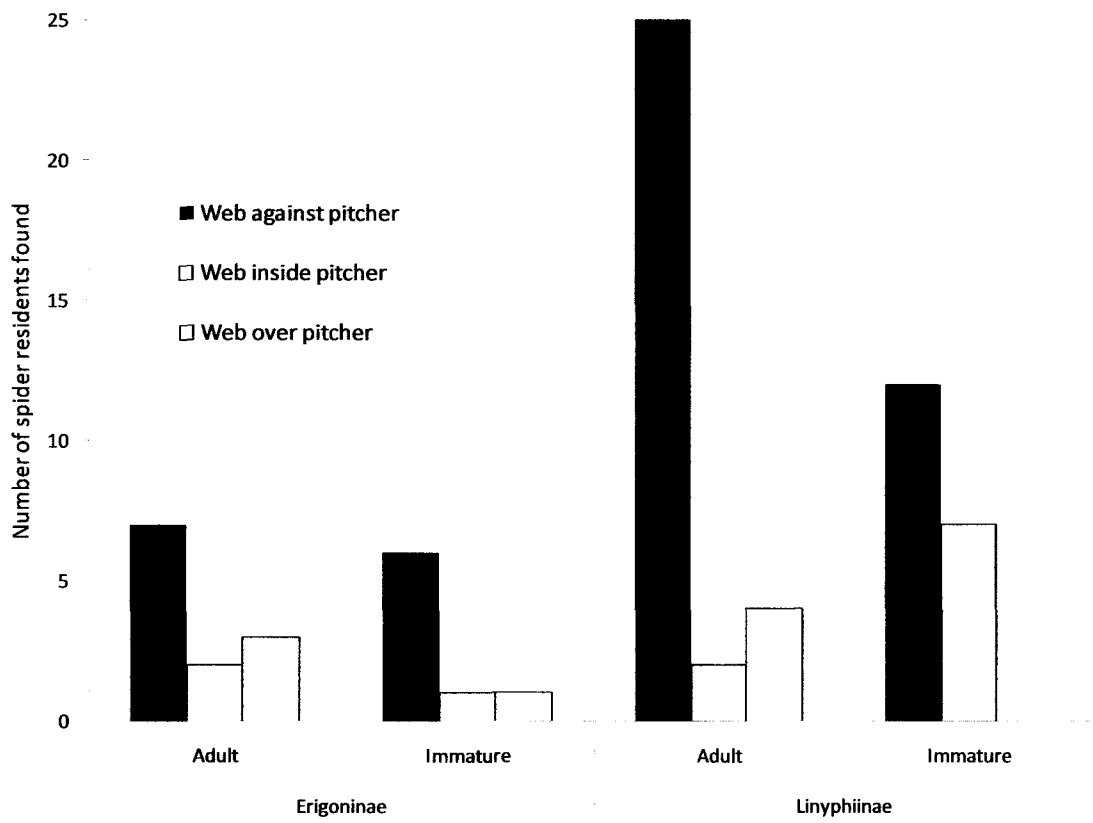


FIG. 30. Number of webs built by both linyphiid subfamilies over all treatments.

of erigonine found captured in treatments than residing over them ($t = 3.19$; df = 43; $P = 0.003$) (Fig. 30). Within the linyphiines, adults tended to prefer to build webs against the pitcher and were hardly ever found in webs inside the pitchers while spiderlings built webs both against the pitcher and inside the pitchers. Other resident web-building arachnids included adult and immature agelenids (1), araneids (1), tetragnathids (1), theridiids (3), and unknown spiderlings (9). Approximately half of all of the arachnids in these webs were adults (49.5%) and the other half were immatures (50.5%).

**Discussion**

These data show that: 1) pitcher structure alone is not sufficient to effectively capture prey, as evidenced by the model data; 2) pigment plays little role in overall prey attraction / retention; 3) plants lacking peristome nectar (N-P+W+) are still able to capture a large number of prey; 4) newer pitchers capture more arachnid and non-arachnid prey than older pitchers; 5) older pitchers are as ineffective at prey capture as models; 6) arachnids act similarly to non-arachnids near pitcher plants; 7) captured arachnids tend to be adult males that do not build webs; 8) web-building arachnid residents do not use *S. purpurea* morphological features (nectar, pigment, or decaying prey) as cues for web construction, although pitcher structure may play a part in web-site selection; 9) among the linyphiids, the linyphiines are more likely to be residents than prey while the erigonines are more likely to be prey than residents.

Models performed poorly compared to new pitchers of other treatments. These data reflect the results from similar studies that used pitcher plants models (Bhattarai 2007, Bhattarai and Horner 2009). The lack of success of the models in prey capture may highlight the importance of *S. purpurea*'s morphological features in new pitchers in capturing arthropod prey. Although there were differences between the real plants and the models in color and the lack of downward facing hairs, the general structure was the same. In addition, studies that used green-colored models found similar results (Bhattarai and Horner 2009). Moreover, waxy surface and

hairs were present in older pitchers, which performed similarly to models in prey capture in this study.

The lack of statistical difference in prey capture between N+P+W+ and N+P-W+ indicates that pigment had little effect in attracting / retaining prey in *S. purpurea*, an idea supported by studies comparing pigmented to non-pigmented *Sarracenia* varieties (Sheridan et al. 2000, Schnell 2002, Green and Horner 2007). However, other studies using *S. purpurea* showed that pitchers with a greater amount of red venation caught more prey (Cresswell 1993, Newell and Nastase 1998). Clearly, there is much to learn about non-pigmented varieties of pitcher plants and their abilities to attract / retain prey.

The N-P+W+ was effective at capturing a large number of prey in the absence of a nectar lure on the peristome. This coating often killed the peristome tissue, indicating that stomata, and undoubtedly any other glands, were unable to function beneath the substance. Indeed, insects were never observed drinking nectar from the peristome of these plants although this was commonly seen in unmodified plants. However, prey may have been attracted to or retained by nectar glands present along the entire exterior of the pitcher (Russell 1919, Juniper et al. 1989). Although exterior glands may have also exuded nectar, there was less nectar available in N-P+W+ plants than N+P+W+. Cresswell (1993) found that pitchers with more available nectar captured more prey, but these data do not support this conclusion.

New pitchers were more effective at capturing non-spiders and spiders than older pitchers. In fact, old pitchers were as ineffective at capturing prey as models, suggesting that these older pitchers lack any functioning morphological features. The difference in capture of specific taxa by new and old pitchers was largely significant. Two of the groups that did not share this pattern were collembolans and acari. These taxa are ubiquitous at high densities in most environments (Triplehorn and Johnson 2005) and this may cause a high number of random catches by *S. purpurea*, regardless of pitcher age.

Although new pitchers have been shown to capture a higher density of insects (Fish and

Hall 1978), this is the first time it has been quantified for a local arachnid population. The similar capture pattern between arachnids and non-arachnids suggests similarities between these groups in their approach to the plant's morphological features. Another possible explanation for this correlation is that arachnids are found near areas of high prey density and therefore encounter the same vegetation most non-arachnids encounter, a conclusion reached by Nentwig (1982) who studied correlations between common prey and wandering spider densities found in pitfall traps. However, arachnid residents were not found near plants that captured more prey. The simultaneous sampling of arachnid residents and prey may have also suppressed the number of arachnids captured.

There were distinct differences among arachnid taxa in their tendencies to be residents or prey, although the sampling method of residents may have been biased towards female web-builders because transient ground spiders and harvestmen were less likely to be found than a sedentary web-residing spider within the short time the plants were sampled. Ground spiders such as corinnids, lycosids, and salticids were more common as prey while web-building linyphiines were more often residents. In addition, male arachnids tended to become prey more often than females. The increased capture density of male spiders may be due to a tendency for males to wander and look for mates (Foelix 1996), contact, and fall into pitchers more often. Female spiders lead a more sedentary lifestyle (Foelix 1996), and are likely to be found as residents in webs.

Spiders readily drink sugar-laden liquids, including *S. purpurea* nectar, in the laboratory (Pollard et al. 1995, Amalin et al. 2001, Jackson et al. 2001, Taylor 2004) yet appear unaware of its presence until contact is made (personal observation). These data suggest that spiders may not be lured by nectar from afar, but rather, become victims of their wandering behavior and/or their serendipitous discovery of nectar. At least some spiders can see in the UV spectrum (Yamashita and Tateda 1976, Lim and Li 2006) so it is also possible that spiders are attracted to pitchers with prominent UV patterns, which may be enhanced by pigment and/or nectar (Joel et al. 1985).

The role of arachnids when encountering *S. purpurea* seems to be one of prey or non-selective web-builder (in terms of *S. purpurea*'s morphological features) rather than an opportunistic kleptoparasite that seeks out plants with high amounts of prey (Cresswell 1991, 1993). There was no difference among treatments in the density of arachnid residents found, indicating that arachnids were non-selective for the presence of specific *S. purpurea* morphological features when choosing a living site. This lack of preference also existed between those treatments that held dead prey and the cotton-filled pitchers that lacked prey, indicating that arachnids did not select treatments based on high prey capture densities. Similarly, Cresswell (1993) found that spider residency was not correlated to any *S. purpurea* morphological features other than pitcher size.

Small, sheet-web building erigonines were more often prey than residents, in contrast to the pattern found in the linyphiines. Erigonines often created webs against and inside pitchers. As adults, these spiders commonly build webs of 3 $cm^2$ (Sunderland et al. 1986a) - 8 $cm^2$ (Harwood et al. 2001), a range similar to the mean area inside the pitchers in the treatments (7.69 $cm^2$). Therefore, the reason of residency inside pitchers may have been for architectural reasons. Since erigonines are more prone to hunt for prey at the edges of their web compared to linyphiines (Harwood et al. 2003), this behavior may have contributed to accidental falls into the pitcher depths. In addition, larger prey falling into or struggling within the pitcher may have caught the web and brought the spider along with it.

Linyphiines often built webs inside the pitchers as spiderlings. These spiders generally occur in webs ~10cm from the ground (Sunderland et al. 1986b) and choose web-sites based on the presence of vertical structures to support their webs (Samu et al. 1996, Halaj et al. 2000) and the amount of food in the habitat (Harwood et al. 2001, 2003). Adult linyphiines build webs from 16$cm^2$ (Sunderland et al. 1986a) - 74$cm^2$ (Harwood et al. 2001) in size and spiderlings undoubtedly build a smaller web. Linyphiine spiderlings were often found in webs inside pitchers, but not adults. Similar to the erigonine adults, this behavior may have contributed to

their high percentage of capture by *S. purpurea*. Therefore, although there was a lack of selection for residency near specific treatments due to a difference in the plant's morphological features, there seemed to be a selection by erigonines and linyphiine spiderlings for the unique architecture of *S. purpurea* pitchers. In addition, only one agelenid spider was found during the study (an *Agelenopsis* spiderling) which had built a funnel web emanating from a N-P-W+ pitcher. These spiders commonly build funnel webs that lead into *S. purpurea* pitchers (personal observation).

Although carnivorous plants' morphological features have been believed to play a major role in prey attraction and retention (Darwin 1875, Lloyd 1942, Joel 1986), hypotheses of random capture have also been suggested (Williams 1976, Lichtner and Williams 1977, Zamora 1995, Schnell 2002). New pitchers caught significantly more prey than old pitchers and models, indicating an increased attraction / retention ability for new pitchers. However, no difference in capture was found between pigmented and non-pigmented new or old pitchers, indicating no discernable effect of pigment. Similarly, no difference in capture was found between unsealed peristome and sealed peristome new or old pitchers, indicating no discernable effect of peristome nectar. However, it is possible that pigment and nectar had similar effectiveness but were not additive. If this were the case, then treatments with either pigment or nectar (N+P+W+, N-P+W+, N+P-W+) could effectively catch prey while those lacking both of these features (N-P-W+) could not; this was indeed witnessed in this study. The similarity in capture between N+P+W+, N-P+W+, and N+P-W+ may have also been due to the presence of an untested attractant / retainer present in all three treatments such as fragrance or an attractive UV pattern (Joel et al. 1985, Schnell 2002).

# CHAPTER VII

## SPIDER RESIDENCY CONTRIBUTES NUTRIENTS TO THE PURPLE PITCHER PLANT, *SARRACENIA PURPUREA*

### Introduction

Animals that indirectly affect the plant-prey relationship of carnivorous plants have been hypothesized to include spiders (Cresswell 1991, 1993), frogs (Schnell 2002), and slugs (Zamora and Gomez 1996). Spiders often play indirect roles in carnivorous plant-insect mutualisms such as stealing prey (Fage 1928, Cresswell 1991, Anderson and Midgley 2002) or consuming plant-defending insects (Gastreich 1999). There are also examples whereby spiders directly defend carnivorous and nectar-bearing plants in facultative mutualisms (Whitney 2004, Romero et al. 2008). The dynamics of nutrient exchange between many carnivorous plants and associated organisms have been quantified (Ellis and Midgley 1996, Anderson and Midgley 2002, 2003), yet those concerning North American pitcher plants and their associated organisms remain largely uninvestigated.

Interactions between *S. purpurea* and its prey (Wray and Brimley 1943, Judd 1959, Cresswell 1991, Heard 1998) and phytotelmatous community (Bradshaw and Creelman 1984, Cochran-Stafira and von Ende 1998, Hamilton and Duffield 2002, Mouquet et al. 2008) have been studied to some length. However, the interaction between spiders and *S. purpurea* has largely been ignored. The few studies that have investigated this relationship have focused on spiders as prey (Wray and Brimley 1943, Judd 1959, Heard 1998) and only a few have studied spiders as opportunistic ovipositors (Rymal and Folkerts 1982) or kleptoparasitic residents (Cresswell 1991, 1993). Kleptoparasitism has been noted for linyphiids, but quantification of nutritional benefit to the plant was not done (Cresswell 1991, 1993). It has been postulated that the relationship between spiders and *S. purpurea* may be mutualistic, as dropped frass, prey,

exuvia, web debris, and webbing may all contribute nitrogen to pitchers during spider residency (Schnell 2002).

In addition to the linyphiids, the agelenids also build webs over *S. purpurea* (Milne *unpublished data*). These spiders commonly build large sheet webs over grass, within footprints, and over general vegetation (Riechert 1974, Foelix 1996). The sheet web converges into a funnel that serves as a retreat for the spider. When prey land on the non-sticky web, the vibrations cue the spider that an insect is trapped, and the spider runs from the retreat and injects it with venom (Foelix 1996). After envenomation, the prey is dragged to the retreat and consumed (Nentwig 1983). After feeding, unconsumed parts are often left near the edge of the retreat (personal observation). When an agelenid takes up residency on a pitcher, the entire pitcher opening is covered by webbing (personal observation).

*Sarracenia purpurea* uses captured arthropods mainly to supplement low nitrogen levels in its boggy environment (Ellison and Gotelli 2002). *Sarracenia purpurea* gets very little of its nitrogen from its root system (Butler and Ellison 2007). The plant is composed entirely of prey-capturing leaves of various ages. New pitchers arise from the center of a whorl that is flush with the ground. Most prey is captured by newer, younger pitchers within the first 30 days of opening (Fish and Hall 1978). *Sarracenia purpurea* creates new pitchers starting in May and lasts throughout the summer (Schnell 2002). Pitchers created early in the growing season retain approximately 8% of their nitrogen and the rest is translocated to newer pitchers. Pitchers produced later in the growing season retain most of their prey-derived nitrogen (Butler and Ellison 2007).

The use of stable isotopes, specifically $^{15}N$, in studies concerning carnivorous plants have usually concentrated on the nutrition gained from prey (Schulze et al. 1991, Friday and Quarmby 1994, Moran et al. 2001, Schulze et al. 2001, Anderson and Midgley 2002, 2003, Millett et al. 2003, Glassman 2007). A few studies have used stable isotopes to investigate the indirect interactions of spiders with carnivorous plants (Anderson and Midgley 2002) and nectar-bearing

shrubs (Whitney 2004). However no study has investigated the direct contribution of spiders to the nutrition of a carnivorous plant.

The hypothesis of this chapter is that spiders contribute nutrients to *S. purpurea* pitchers. This was tested by using stable isotope signatures to determine if spider residency results in a net increase or decrease of nitrogen in pitchers of *S. purpurea*. In addition, the frequency of pitcher habitation by agelenids was recorded from observations in the field. The stable isotope signature of directly-fed pitchers was compared to pitchers fed spider-resided filters and control pitchers to determine if spider residency contributed to pitcher nutrition and if the net exchange due to spider residency was negative or positive. In addition, the capture area and efficiency of the spider, *Agelenopsis*, was compared to that of *S. purpurea* to determine if, in certain situations, *Agelenopsis* residency may actually be beneficial to the plant.

**Methods**

Agelenid spiders were collected from webs in pitchers of *S. purpurea* at the Blackwater Ecologic Preserve in Isle of Wight County, Virginia (36.87° N, 76.83° W). This 319 acre preserve is a fire-dependent community dominated by turkey oak (*Quercus laevis*) and loblolly pine (*Pinus taeda*), with many herbaceous shrubs and open spaces with low lying plants (Frost and Musselman 1987). Approximately 15 – 25 naturally occurring clumps of *S. purpurea* grow in the preserve.

Each *S. purpurea* clump was checked for agelenid residents once a month for 13 months. Spiders were collected from January 2006 – January 2007. When found, spiders were sampled using a mechanical aspirator (2820A AC Insect Vaccum, Bioquip Products, Inc. Rancho Dominguez, CA) and preserved. Spider identifications were done using Chamberlin and Ivie (1941) and Ubick et al. (2005).

Twenty-five *S. purpurea* were obtained from Meadowview Biological Station in Woodford, VA. Plants were grown in Canadian sphagnum peat moss and locally harvested

(Caroline County, VA) silica masonry sand mixture in a 50:50 ratio. Plants were grown outside in water tanks that maintained a level 1/3 the pot height, grown in full sun, and the water source was a local, tannic, dystrophic pond before use in this study. The *S. purpurea* were housed in a large greenhouse at Old Dominion University (ODU) in a 50/50 mixture of Canadian peat moss and sand, with a 12/12 light regimen and were watered daily. Due to the possibility of nitrogen translocation from the previous season's pitchers to the current season's pitchers (Butler and Ellison 2007), each plant was trimmed down to five pitchers and older pitchers were removed when new ones appeared, limiting nutrient translocation.

*Agelenopsis* were collected from the ODU campus and were placed in separate containers. All spiders were starved for one week prior to testing to allow for all field-consumed prey to move through their digestive systems. Ten spiders taken from the same habitat were raised to adulthood and identified.

Two-hundred and fifty crickets (*Acheta domesticus*) were kept in a large Tupperware container (0.6m x 0.4m x 0.17m) and were fed a 50/50 mixture of cornmeal (Yellow Corn Meal, Quaker, Chicago) and wheat gluten (Vital Wheat Gluten Flour, Bob's Red Mill, Milwaukie) along with a constant supply of water. After all crickets had molted at least once, crickets of approximately 1.5 cm in length were used for feeding plants and spiders.

Pitchers formed late in the growing season (August) were used throughout the experiments to reduce the amount of nitrogen translocated from earlier pitchers (Butler and Ellison 2007). Six pitchers were half-filled with distilled water and fed one cricket per week over three weeks (8-15-08, 8-25-08, and 9-2-08). Pitchers were allowed to digest their prey for two weeks prior to being emptied, dried in a heating oven (Cat. No. 1483, Precision Scientific Co., Chicago) at 40°C, and prepared for analysis.

Six spiders (all *Agelenopsis*) were haphazardly chosen (fed spiders) and placed in vials (278.8 $cm^3$). Each vial had its bottom lined with trimmed filter paper (Cat. No. 1001070, Whatman #1, 70 mm). Spiders were allowed to construct truncated webs inside the vials to

simulate the terminal funnel portion of a web. Spiders were fed one cricket per week (8-7-08, 8-13-08, 8-18-08 – except for two spiders, which did not feed on the last date and instead were each fed on 8-21-08 and 8-25-08). After the third week of feeding, spiders remained in the vials for 15 more days so that they could digest prey. Spiders were then removed, killed by placing them in a freezer, and dried in a heating oven (Cat. No. 1483, Precision Scientific Co., Chicago) at 40°C.

Filter papers used during the feeding of spiders, with all webbing, frass, exuvia, and insect debris, were cut into three equal sections. One section was submerged under distilled water inside a new pitcher on a previously unused plant each week for three weeks. The pitchers were allowed to digest the final section of paper for two more weeks before being removed and dried.

To control for the digestion of the filter paper without debris, six new pitchers on previously unused plants were fed equivalent sections of unused filter paper once a week for three weeks and then allowed to digest for an additional two weeks. These pitchers were then removed and dried.

Six spiders were haphazardly chosen (unfed spiders) and were killed after one week of starvation by placing them in a freezer for 1 hr. Spiders were dried in a heating oven (Cat. No. 1483, Precision Scientific Co., Chicago) at 40°C.

To analyze the nitrogen signature of crickets, six were haphazardly chosen, were killed by placing them in a freezer, and dried in a heating oven (Cat. No. 1483, Precision Scientific Co., Chicago) at 40°C.

Two terrariums (0.51m x 0.26m x 0.32m) were filled 1/4 full with a 50/50 mixture of sand and Canadian peat moss. Each terrarium had one *S. purpurea* planted in the center. In each terrarium, a newly opened pitcher was cornered off with modified pieces of plastic so that only that pitcher was available for residence. Two *Agelenopsis* (one per terrarium) were allowed to build webs inside the cornered-off area that funneled into the pitcher. Webs that were built in other locations were destroyed. While residing in their webs, spiders were fed one cricket per

week for three weeks. Spiders were allowed to feed on and move their prey, molt, excrete, and act without restriction. One week after the last cricket was fed to each spider, each *Agelenopsis* was removed. Pitchers were then half-filled with water and all organic matter was flushed into the pitchers, simulating rainfall. The pitchers were then removed one week later, and dried.

This experiment created seven different types of samples (Fig. 31). All samples were dried in the same heating oven at 40° C for at least two weeks. Samples were then weighed and ground using a mortar and pestle. These samples were then placed into tin capsules in a 96-well plate and sent to the Berkeley Stable Isotope Laboratory in Berkeley, CA for $\delta^{15}N$ analysis.

Tests for normality and homogeneity of variance were conducted before each statistical study. If data did not meet these standards, they were transformed. All data were considered significant when $P < 0.05$. Independent samples t-tests were conducted to compare the stable isotope signatures between unfed and fed spiders. Tretments were compared using a one-Factor ANOVA with a Tukey's multiple comparisons post-hoc test.

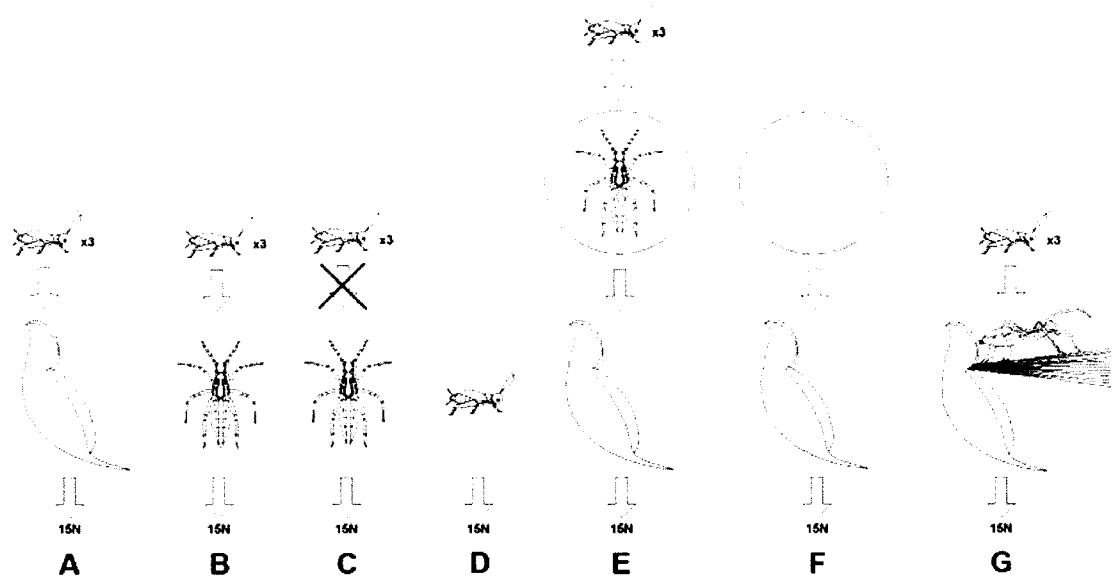


FIG. 31. The seven types of samples analyzed for their $\delta^{15}N$ signature. A = direct-fed pitchers; B = cricket-fed *Agelenopsis*; C = unfed *Agelenopsis*; D = crickets; E = pitchers fed *Agelenopsis*-resided filter paper; F = pitchers fed control filter paper; G = pitchers with *Agelenopsis* residents.

**Results**

Fifteen agelenid spiders residing on *S. purpurea* were collected over 13 months (Fig. 32). Three more agelenids were recorded as having webs leading into pitchers but escaped capture. All fifteen spiders were immature and not identified to species. Spider residents were often found

FIG. 32. An *Agelenopsis* residing inside a *S. purpurea* pitcher.

with remains of prey, such as exoskeletons and butterfly wings, in their web near the pitcher opening. Some *Agelenopsis* webs covered only the resided pitcher while others covered multiple pitchers. Other *Agelenopsis* were observed to build webs leading into crevices between pitchers.

The feeding regimen for the crickets resulted in a high $\delta^{15}N$ signature (6.56‰ ± 0.182 SE). This high nitrogen signature was transferred to the spiders when consumed (6.69‰ ± 0.2 SE). There was a significant increase in the $\delta^{15}N$ value ($t = 5.287$; df = 12; $P < 0.001$) between fed and unfed spiders.

The sampling of 15 pitcher plants once a month for 13 months (January was sampled twice) produced 195 sampling attempts. 18 instances of spider residency were recorded, resulting

in a 9.2% residency rate of funnel web spiders per pitcher plant at BEP. Agelenid residents were most often found during August and January. However, 50% of residencies occurred in the late summer and early fall: from July – October (Fig. 33).

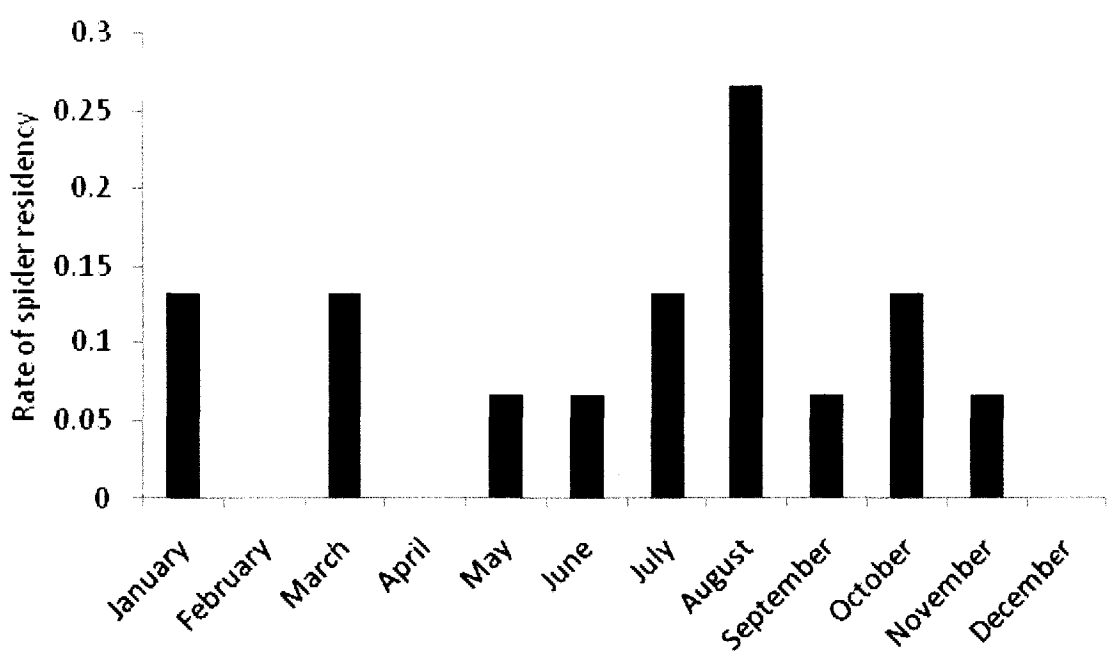


FIG. 33. Rate of spider residency (# of Agelenid spiders found / # of pitcher plants sampled) per month at BEP.

There was a significant difference among the four pitcher samples (Fig. 31: A, E, F & G) in $\delta^{15}N$ ($F = 7.91$; $df = 3, 19$; $P = 0.002$). The pitchers fed control filter paper had significantly lower $\delta^{15}N$ values compared to the pitchers fed treatment filter paper (Tukey's HSD: $P = 0.028$), direct-fed pitchers (Tukey's HSD: $P = 0.003$), and spider-resided pitchers (Tukey's HSD: $P = 0.014$). All other relationships among treatments were non-significant (Fig. 34).

**Discussion**

Agelenid residency on *S. purpurea* occurred during approximately 9% of the sampling instances at BEP. However, this phenomenon may occur at even higher rates if pitcher plant

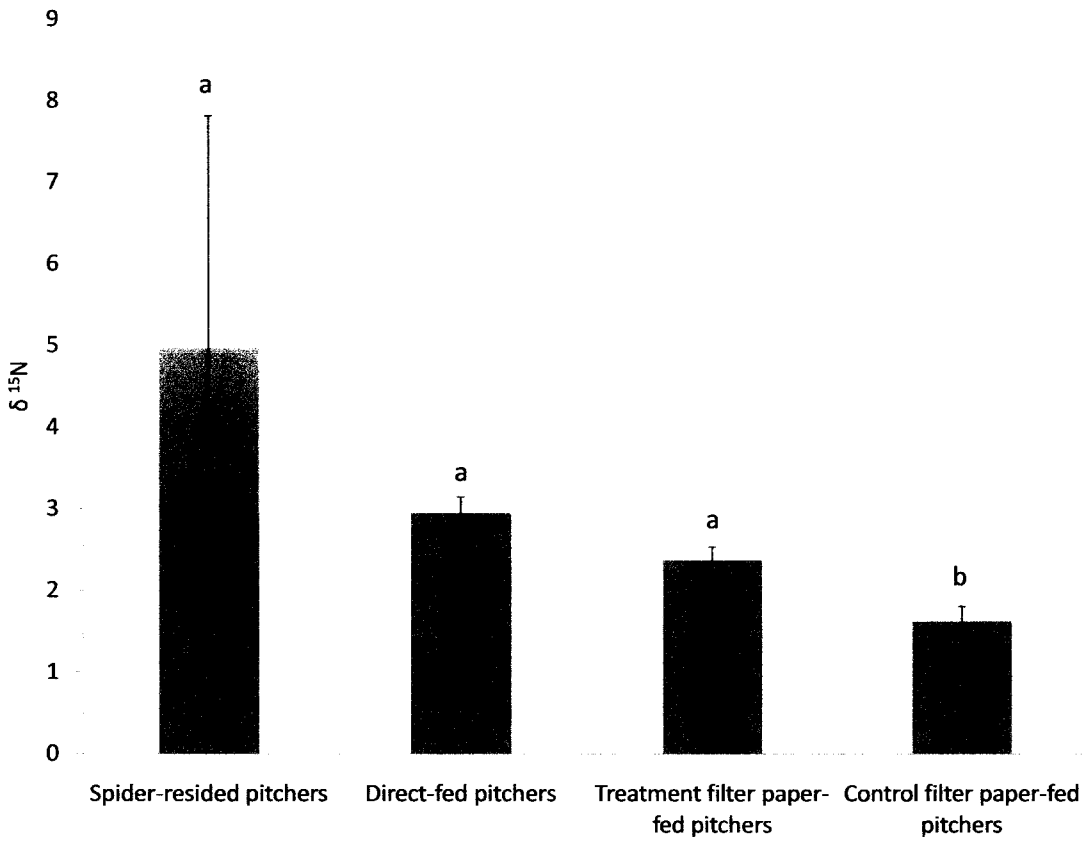


FIG. 34. Comparison in the $\delta^{15}N$ signature ± SE among various pitchers. Letters indicate significant differences at $P = 0.05$.

populations are at larger densities. Funnel-weaving spiders are most dense from June – September (Howell and Jenkins 2004) and this density is reflected in their high rate of residency at BEP during this time period.

Spider residency can contribute nutrients to the plant. This result contrasts with the studies by Cresswell (1993) that assumed that spiders were kleptoparasitic and harmed the plant by reducing prey capture. Spider residency, especially concerning *Agelenopsis*, probably reduces direct prey capture by *S. purpurea*, but may not significantly affect nitrogen intake. Since carnivory evolved to counteract nitrogen deficiency (Juniper et al. 1989), nitrogen intake, not biomass intake, should be the determinant of whether or not a relationship between spiders and pitcher plants is beneficial to *S. purpurea*. If prey intake is reduced to zero but nitrogen intake is

increased, the plant is most likely benefiting from the relationship.

On first examination, the similarity between fed and resided pitchers in their $^{15}N$ signatures seems to suggest that a commensalism exists between *S. purpurea*, which is unaffected by *Agelenopsis* residency, and *Agelenopsis*, which receives a home that may attract prey (Juniper et al. 1989). However, this comparison assumes an equal rate of prey capture among participants. In contrast, the rate of prey captured between *S. purpurea* and *Agelenopsis* may be widely different in a given time period depending on physiological, environmental, and behavioral factors such as humidity and time of day (Schnell 2002, Wise 1993, Ellison and Gotelli 2009). For example, old *S. purpurea* pitchers capture almost no prey (Fish and Hall 1978) and an *Agelenopsis* resident would undoubtedly increase the rate of prey capture for these older leaves.

One factor that affects prey capture is the size of the capture area. The mean size of the pitcher opening of all plants tested in the current study was 2.1 $cm^2$ while the mean size of a web (*Agelenopsis aperta*) ranges from 113 $cm^2$ (immatures) to 506 $cm^2$ (adults) (Riechert 1974). Since most of the residents occurring on *S. purpurea* in the field were immature, the lower value of web size may be used for comparison and therefore the capture area of an *Agelenopsis* web is approximately 54 times larger than that of *S. purpurea*. If there is no difference in nitrogen intake between pitchers fed directly and those with an *Agelenopsis* resident, then a *S. purpurea* pitcher increases its effective capture area by 54 times by having an *Agelenopsis* resident.

A second factor that may affect prey capture is the efficiency of each capturing mechanism. A *S. purpurea* pitcher is between 0.83% - 0.93% efficient at prey capture, depending on the definition of 'prey' (Newell and Nastase 1998). In contrast, *Agelenopsis aperta* is approximately 60% effective at prey capture (Riechert and Tracy 1975). Therefore if an *Agelenopsis* web funnels into a *S. purpurea* pitcher, not only does the pitcher increase its capture area by having this resident, it may also increase its effectiveness at capturing prey.

A confounding factor that may interfere with the benefit analysis to *S. purpurea* from *Agelenopsis* residency is that sometimes *Agelenopsis* creates a funnel web that leads out of a

pitcher and the bottom sheet of the web spans over other pitchers on the same plant. Although this does not reduce the effective capture area of the resided pitcher, it most likely reduces the capture efficiency of the other pitchers on the plant, thereby reducing the nitrogen intake of the plant as a whole. Moreover, the *Agelenopsis* that resided in funnels that covered pitchers and led into crevices between pitchers did not benefit the plant at all and were almost certainly kleptoparasitic.

*Agelenopsis* may contribute nitrogen to *S. purpurea* pitchers through frass, insect carcasses, or silk. If prey are high in nitrogen, then frass may also be high in nitrogen. Insect exoskeletons are constructed of mainly chitin, yet the soft tissue in the joints can easily be digested by pitcher liquid-enzymes (Schnell 2002). Moreover, the liquid in pitchers contains chitinase (Schnell 2002). Therefore, insect exoskeletons may be probable sources of nitrogen for the plant. Spider silk is proteinaceous and is composed of nitrogen-containing amino acids (Foelix 1996). Although *S. purpurea* possesses digestive enzymes (Gallie and Chang 1997) and bacteria within the pitchers, much of the digestion may be done by *Agelenopsis* prior to entering the pitcher. If frass is the main source of the $^{15}N$ (as opposed to silk or exuvia), then the interaction may be considered a digestive mutualism whereby *Agelenopsis* digests prey for the plant (Anderson and Midgley 2003). Future research may reveal the specific source of the nitrogen, although silk and frass washed or dropped into the pitcher are the two likely sources.

It is unknown if *Agelenopsis* actively chooses *S. purpurea* pitchers as a web site over other sites, yet the architecture of *S. purpurea* pitchers is unlike the structure of other surrounding vegetation. Since agelenids commonly select habitats based on vegetation structure (Riechert 1974), the architecture of the plant may cause these spiders to build their webs over *S. purpurea*. Indeed, polyurethane models of *S. purpurea* pitchers left in funnel-weaving spider habitats have quickly gained residents (Milne, unpublished data). The relationship between *Agelenopsis* and *S. purpurea* may therefore closely resemble a facultative mutualism whereby *Agelenopsis* gains a favorable place to live while *S. purpurea* gains an increase in nitrogen.

# CHAPTER VIII

## *SARRACENIA PURPUREA* AS A SPIDER OVIPOSITION SITE

### Introduction

Spiders employ a range of behaviors to protect their egg sacs. They place them in webs or silk-lined tunnels, under stones or bark, or in rolled-up leaves; they grasp them with their chelicerae or attach them to their own abdomens (Foelix 1996). Silk cocoons surround the eggs to help prevent water loss, desiccation, and changes in temperature and humidity. Although the cocoon's silk also aids in defense against predatory organisms, adults of certain species often take up residency near the cocoon in order to further aid in the survival of the juveniles (Foelix 1996). Maternal care for the cocoon among spider species ranges from complete abandonment to guarding and aiding in opening (Foelix 1996).

Many spiders are deliberate and selective in their web placement (Enders 1977, Suter et al. 1987) and some have been shown to associate with carnivorous plants, usually as either kleptoparasites (Rymal and Folkerts 1982, Cresswell 1991, 1993, Anderson and Midgley 2002, Schnell 2002) or prey (Wray and Brimley 1943, Judd 1959, Heard 1998). The carnivorous purple pitcher plant, *Sarracenia purpurea*, is a low-lying herbaceous plant that uses water-filled pitcher-shaped leaves to trap, kill, and digest arthropod prey (Schnell 2002). Pitchers catch the most prey during the first two weeks of opening (Fish and Hall 1978), yet they persist during the full growing season, often in a slowly senescing state whereby the pitcher leaf decays from the top down over the course of the year (Schnell 2002).

A variety of flying insects regularly oviposit in the liquid of *S. purpurea* pitchers, creating a phytotelmatous community. These include larvae of the mosquito, *Wyeomyia smithii*, the midge, *Metriocnemus knabi*, and flesh flies, *Fletcherimyia fletcheri* and *Sarcophaga sarraceniae*. However, the only known organism that commonly utilizes an entire dry pitcher as

its home is the pitcher plant moth (*Exyra* sp.), which spins cocoons inside first-year *S. purpurea* pitchers (Schnell 2002). This demonstrates a parasitic relationship (Schnell 2002), while the plant's relationship with the macroinvertebrate phytotelmatous community has been shown to be at least partially mutualistic (Bradshaw and Creelman 1984, Mouquet et al. 2008). For spiders, the use of *S. purpurea* pitchers as oviposition sites has been noted for only one family of spiders (Lycosidae) (Hubbard 1896, Jones 1935), although Rymal and Folkerts (1982) note this relationship for an unspecified *Sarracenia* species.

The goal of this study was to test the hypothesis that spiders commonly use *S. purpurea* as an oviposition site. A secondary hypothesis was also tested: spiders oviposit more often in senesced pitchers than new pitchers. Surveys of two pitcher plant locations at two locations were conducted in order to properly prove or disprove these hypotheses.

**Methods**

The Highlands Botanical Station (HBS, 35.05° N, 83.19° W) in Highlands, NC, and the Joseph Pines Preserve (JPP, 37.05° N, 77.24° W) near Waverly, VA, were searched for spiders residing in the pitchers of *S. purpurea*. HBS was sampled once a week through eight weeks in June and July, 2007 and JPP was sampled once a month for six months from April – September, 2008. The sampled area at the Highlands Biological Station is a marshy area on the outskirts of the 0.045 $km^2$ garden, containing approximately 700 *S. purpurea* clumps along a lake edge. The Joseph Pines Preserve is an artificially managed, periodically burned, 0.4 $km^2$ site that contains approximately 100 S. purpurea clumps.

During each sampling period, all pitcher plants at the preserve were checked for spider residents with cocoons. When spiders were found, they were collected and preserved for later identification. The number of egg sacs held by each spider was counted. The level of senescence for each resided pitcher was determined through observation and recorded.

**Results**

Twelve *Enoplognatha caricis* (Theridiidae) (Fig. 35), eight *Pirata insularis* (Lycosidae),


FIG. 35. Adult female *Enoplognatha caricis* living inside a senescing pitcher of *S. purpurea* with four cocoons (c).

two *Theridion frondeum* (Theridiidae), one *Eperigone maculata* (Linyphiidae), and one *Clubiona rhododendri* (Clubionidae) adult females were observed with cocoons inside *S. purpurea* pitchers in Highlands, NC while one adult female *Hogna rabida* (Lycosidae) (Fig. 36) was observed residing in a pitcher at the Joseph Pines Preserve. All spiders were seen with cocoons either attached to the inner walls of the pitcher or, regarding the Lycosidae, attached to the spider's abdomen. The number of cocoons held by each spider varied by taxa; the number of cocoons held by *E. caricis* ranged from 1-5 (mean = 1.5, SD = 1.17, mode = 1) and the *E. maculata* was

FIG. 36. Adult female *Hogna rabida* living inside a senescing pitcher of *S. purpurea.*

seen with three cocoons while all other spider types were seen with only one cocoon each (Table 14). All spiders were observed to be residents of the pitchers as opposed to prey, as webbing spanned the inner aperture of the pitchers, seeming to prevent the spiders' capture and allowing them to move freely around and out of the leaf. All spiders were found inside partially- or fully-senesced pitchers.

TABLE 14. Species of spiders found with egg sacs in *S. purpurea*.

| Species | N | Mean number of egg sacs |
|---|---|---|
| *Clubiona rhododendri* | 1 | 1 |
| *Enoplognatha tecta* | 12 | 1.5 |
| *Eperigone maculata* | 1 | 3 |
| *Hogna rabida* | 1 | 1 |
| *Pirata insularis* | 8 | 1 |
| *Theridion frondeum* | 2 | 1 |

**Discussion**

Spiders make up a large proportion of the arthropod prey captured by *S. purpurea* (Wray and Brimley 1943, Judd 1959, Heard 1998). Therefore, if spiders were to build webs in actively trapping pitchers, they must first prevent capture and make the pitcher safe for residency. This precaution may be why the spiders observed in this study resided in senesced pitchers – pitchers that no longer posed a significant threat to arthropods (Fish and Hall 1978).

Only a few scattered reports exist of spiders using carnivorous plants as oviposition sites (Hubbard 1896, Jones 1935, Rymal and Folkerts 1982). Spiders residing in *S. purpurea* may gain an advantage over spiders using other microenvironments to raise their young. Pitchers are protected on three sides by the inner leaf surface. These leaves may present a microenvironment similar to the funnel webs of *Agelenopsis* or *Sosippus*, which are covered laterally by webbing and have a rear retreat (Brady 1962, Foelix 1996). Spiders of the genus *Agenelopsis* build funnel-webs that funnel into *S. purpurea* pitchers and spiders often retreat to the bottom of the pitcher when disturbed (personal observation). *Sarracenia purpurea* pitchers may present an ideal architectural refuge for spiders seeking shelter from predators or protection for their young. This may be particularly useful in bog habitats where protective vegetation is scarce.

# CHAPTER IX

## CONCLUSIONS

Spiders and harvestmen may engage in one of four types of ecological relationships with *Sarracenia purpurea*, including predator and prey (Wray and Brimley 1943, Heard 1998), kleptoparasite and host (Cresswell 1991, 1993), mutual beneficiaries (mutualism), or beneficiary and unaffected host (commensalism). The type of relationship in which the two actors engage is dependent on many factors, including the family, maturity level, and sex of the spider involved, the age of the pitcher, and the amount of nectar on the pitcher.

The most prevalent kind of ecological relationship between spiders and *S. purpurea* is that of predator and prey. Unlike most plant / animal interactions where plants are preyed upon by animals, in this relationship, *S. purpurea* acts as the predator and the spiders and harvestmen act as the prey. In the present study, the most common spider prey were the most common in the surrounding environment (e.g. Linyphiidae, Lycosidae, and Salticidae). Similar observations have been made for insect communities in *Drosera* habitats, in which the diversity of insects in the environment corresponds to the captured insect diversity (Achterberg 1973). However, there were several exceptions to this trend.

Some families of spiders (e.g. the ground spiders, Corinnidae and Gnaphosidae) were captured by *S. purpurea* in much higher proportions in the surrounding environment (Foelix 1996). Other ground spiders that were common in the environment (e.g. Lycosidae, Hahniidae, and Salticidae) were found at equal densities in the environment and as prey inside pitchers, providing evidence towards the third hypothesis. Therefore, the phenomenon of becoming prey of the plant may not be a product of belonging to a specific family as living in a similar niche. Ground spiders may encounter the low-lying *S. purpurea* more often than do web-builders, therefore exposing the ground spiders to more opportunities to become prey.

Several spiders (e.g. Araneidae, Pisauridae, and Thomisidae) had very high densities in the environment but were rarely found as prey. The orb-weaving spiders, Araneidae, commonly build vertical webs at elevated heights (Enders 1974), so that the density of araneids is greater at heights above approximately 1 m than below it. Since *S. purpurea* is a low-lying plant, araneids may not encounter the plant often, and therefore may not be captured in large numbers. Pisaurids are commonly found near water and, more importantly, can just as easily walk on water as they can on the surface of the ground (Foelix 1996). This behavior may allow pisaurids to easily escape capture by *S. purpurea* even if they do commonly encounter the plant. Spiders of the family Thomisidae are crab spiders that are sit-and-wait predators that ambush their prey (Foelix 1996). Thomisids commonly sit and wait on flowers, bushes, and tree trunks (Wise 1993). Although it is unknown why these spiders were not commonly prey, it is interesting to note that crab spiders are kleptoparasites on the edge of *S. purpurea* (Schnell 2002) and *Nepenthes* pitchers (Juniper et al. 1989).

Adult male spiders were more often prey of *S. purpurea* than females. Spider genders in the surrounding environment differed depending on the collection method. Methods that sampled higher vegetation (sweep netting and bush beating) collected a greater number of females than males. The method that sampled the ground (pitfall trapping) collected a greater number of males than females. Since adult male spiders commonly wander great distances looking for females (Foelix 1996), this behavior most likely led to males having a greater capture percentage in pitcher plants and pitfall traps simply due to a higher number of encounters. The high percentage of females collected by sweep netting and bush beating was most likely due to the presence of sedentary females.

Adult spiders were more often captured by *S. purpurea* than spiderlings for almost every spider family. The wandering behavior of adult male spiders was undoubtedly the cause of this trend. The only exceptions to this trend were seen in the Lycosidae and Gnaphosidae. Although it is unknown why gnaphosid spiderlings were found more often than adults, the lycosid behavior

of carrying spiderlings on their abdomen (Foelix 1996) most likely contributed to the high capture rate of spiderlings in pitchers. Adult female lycosids commonly carry their young on their abdomen for several days prior to the spiderlings fending for themselves (Foelix 1996). Therefore, when adult, spiderling-carrying female lycosids fall into pitcher plants, the spiderlings also become victims of her bad decision. This phenomenon inflated the capture data for this spider taxon.

Evidence in the third chapter provided evidence towards one of the sub-hypotheses. The most reliable inter-location predictor of spider diversity captured by pitcher plants was the spider diversity captured by pitcher plants in similar environments. The efficacy of this predictor was dependent on the similarity between the spider diversities in the environments, which undoubtedly varied depending on environmental factors, and ultimately is a factor of the geographic distance between sites. In this way, the farther a pitcher plant population was from a second pitcher plant location, the less accurate the predictor was at determining an accurate measurement of captured spider diversity.

Data in the third chapter supported another one of the sub-hypotheses. The most reliable intra-location predictor of spider diversity captured in pitcher plants was that which was captured in pitfall traps. Pitfall traps have been recognized for their ability to capture a large diversity of ground dwelling-organisms, yet are considered insufficient for sampling other fauna (Adis 1979, Standen 2000). The similarity in the captured spider diversity between pitfall traps and *S. purpurea* indicates that *S. purpurea* specializes on lower-residing spiders and ground spiders. Similar observations concerning *S. purpurea* and other species of *Sarracenia* suggest that pitcher plants may use height to partition limited resources, whereby lower species exploit a different insect fauna than taller species (Gibson 1983). It is unknown if this phenomenon between pitcher plant species also holds true for spider diversity.

Data towards another one of the sub-hypotheses was also provided: a negative correlation existed between the number of pitchers in a clump and the number of spider prey captured per

pitcher by that clump. Therefore, a grouping of pitchers, with supposedly attractive morphological features such as nectar and pigment, did not pose a greater attraction to spiders. This has previously been recorded for insect populations (Gibson 1983, 1991, Zamora 1995). In fact, using three different carnivorous plant species than the one used in this study (*Sarracenia leucophylla*, *Sarracenia alata*, and *Drosera filiformis tracyi*), Gibson (1983) found that the relationship between captured prey per pitcher and the number of pitchers was also negative. Gibson (1983) hypothesized that this phenomenon occurs due to interspecific competition for insect prey among traps of carnivorous plant species. It is likely that the patterns witnessed at BEP, HBS, and JPP are due to intraspecific competition rather than interspecific competition. In addition, the pitchers on the same plant also competed for spider prey.

The first and second hypotheses, that *S. purpurea* affects spider and insect abundance, were rejected by several pieces of evidence found over multiple studies within this dissertation. There was no evidence of attraction of spiders or insects to *S. purpurea*. An attraction between spiders or insects and the plant, would increase spider or insect density near the plant. However, spider density was no different in areas with many pitcher plants versus areas without any pitcher plants. Similarly, insect density was no different near the plant versus far from the plant. These data support observations of prey landing rates near carnivorous plants whereby there was no difference between the carnivorous plant leaves and the leaves of the surrounding vegetation (Zamora 1995, Williams 1976). In fact, Zamora (1995) found that flying insects were more attracted to a nearby non-carnivorous vascular plant than the carnivorous *Pinguicula vallisneriifolia*. These data suggest that nectar and pigment may play a larger role in retaining rather than attracting prey.

Evidence was provided for the fifth hypothesis in chapter six: that the increased rate of spider capture in new pitchers may be directly tied to the increase of retaining features (e.g. nectar and pigment) on the plant. It has previously been documented that nectar is the main "attractant" of prey in *S. purpurea* (Bennett and Ellison 2009). Due to the propensity of insects to consume

nectar, this feature is considered to be the main morphological feature that drives high insect capture in *S. purpurea* (Lloyd 1942, Schnell 2002). Moreover, nectar may also play a larger part in spider nutrition than previously thought (Pollard et al. 1995, Taylor and Foster 1996, Amalin et al. 2001, Jackson et al. 2001, Taylor 2004), including that from *S. purpurea*. Evidence from chapter five showed that spiders and harvetsmen readily drink *S. purpurea* nectar. Although studies have shown that nectar plays a role in prey capture, none have determined if this role is one of attraction or retention. Although a single study demonstrates long-distance olfactory detection of nectar in a single spider species (Patt and Pfannenstiel 2008), most evidence indicates that, for spiders, the role of nectar is mostly one of retention rather than attraction.

An increase in the amount of nectar on a pitcher results in an increase in the number of insect prey captured by that pitcher (Cresswell 1993). Since there was a significant correlation between the insect capture rate and the spider capture rate of individual pitchers, this relationship is hypothesized to also extend to spiders. This correlation may be due to a higher ability of pitchers to retain prey. A general relationship exists whereby the size of an insect is correlated with the amount of nectar needed for detection by that insect (i.e. larger insects can detect only larger amounts of nectar while smaller insects can detect smaller and larger amounts of nectar) (Mailleux et al. 2000). Therefore, if a *S. purpurea* pitcher had more nectar, a greater diversity of prey (large and small insects) may detect the nectar when encountering the leaf, and would therefore remain on the leaf to consume the nectar. This phenomenon would also lead to a greater diversity of prey being captured by plants with more nectar. Similarly, a reduced specialization due to reduced nectar concentration was seen when nectar-reduced pitcher plants were placed side-by-side with normal pitcher plants: nectar-reduced plants were less specialized than normal plants (the probability of an interspecific encounter (PIE) of nectar-reduced plants = 0.51; PIE of *S. purpurea* = 0.61; PIE of *S. purpurea* ssp. *purpurea* form *heterophylla* = 0.68). Nectar-reduced plants captured a higher proportion of ants than either of the full nectar-containing plants (67% vs. 55% (*S. purpurea*) and 43% (*S. purpurea* ssp. *purpurea* form

*heterophylla*)), although this relationship was not statistically significant. Ants are relatively small, and due to their social nature, are common prey of *S. purpurea*; once nectar is detected, ants lead other ants to the source, greatly increasing the number of capture opportunities for the plant. Furthermore, ants' communicatory behavior eliminates the plant's dependency on random encounters for prey capture for this taxon.

Cresswell (1991, 1993) documented the kleptoparasitic nature of spiders near pitcher plants – an ecological relationship whereby spiders live near pitchers as local residents. Linyphiids have been shown to be kleptoparasitic (Cresswell 1991, 1993) in that they build webs directly over or inside the pitchers of *S. purpurea* and capture prey that would have fallen into the leaves (Cresswell 1993). Several other families of spiders also build webs over *S. purpurea*, but linyphiid spiders were shown to be the most common kleptoparasites. These kleptoparasitic spiders do not preferentially select pitchers as web sites based on morphological features such as nectar or pigment. However, the size (Cresswell 1993) and morphology of the pitcher itself (the cup-shape structure of the leaves) may be conducive to certain linyphiid residency; linyphiids in the subfamily Erigoninae build webs of $3cm^2$ (Sunderland et al. 1986a) - 8 $cm^2$ (Harwood et al. 2001), a range similar to the mean area inside the pitchers (7.69 $cm^2$).

As hypothesized in chapter five, an increase in the clumping of pitchers decreased the rate of spider residency per pitcher. This phenomenon was most likely due to a limited number of spiders within a given area. If, as hypothesized, spiders are not attracted to pitchers, the spider residency rate, and therefore the number of webs near pitcher plants, would remain constant. Indeed, spider residency was not affected by the presence or absence of morphological features. At the same time, various numbers of pitchers existed in the environment at any one location. Therefore, as the pitcher density increased, the web density remained unchanged, leading to a decrease in the rate of pitcher residency.

There was no evidence that spiders preferred to build webs near *S. purpurea* due to either the presence of specific pitcher morphological features or the presence of high nearby insect

density, partially rejecting the fifth hypothesis. Resident spiders built webs over and inside models of pitcher plants lacking any hypothesized attractants (e.g. nectar and pigment) just as often as they built webs over real *S. purpurea* plants with all attractants present. This suggests that spiders do not use pitcher morphological features such as nectar and pigment as a web-building cue. There was also no difference in spider residency between pitcher plants that were excluded from catching prey and those that were allowed to catch prey, indicating that spiders did not use captured prey density as a web-building cue. These data indicate that spiders (mostly linyphiids) may act as kleptoparasites on *S. purpurea* in a purely facultative manner. Linyphiids build webs throughout the environment at a relatively stable height (0 – 10 cm from the ground) (Sunderland et. al. 1986a, Harwood et. al. 2001). Since there is no attraction of spiders to the plant, pitcher residency is a product of pitcher height (Cresswell 1993), due to the innate web-building behavior of the spider, not the characteristics of the plant itself.

The sixth hypothesis was shown to be correct: at least one species of spider may act as a mutual beneficiary with *S. purpurea* (mutualism). The funnel-weaving spider, *Agelenopsis*, commonly builds webs that lead into living pitchers (personal observation). Although reducing prey intake, these spiders may increase nitrogen uptake by the plant through excretions, discarded webbing, and insect remains. The spider benefits from this relationship by obtaining a place to spin its web and possibly gaining a safe retreat inside the pitcher. This is the first time a mutualism has been demonstrated between *S. purpurea* and spiders.

As the final hypothesis of this dissertation demonstrated, some spider taxa are involved in a commensal relationship with *S. purpurea* whereby spiders oviposit and live in decayed / decaying *S. purpurea* leaves. In this relationship, spiders gain a hollow structure within which to build a nest for their cocoons. Older, decayed *S. purpurea* leaves do not function in prey capture (Fish and Hall 1978), therefore these ovipositing spiders are not exposed to the dangers of the pitcher leaf. Decayed leaves are brown and not photosynthetic, and are therefore of little use to the plant other than providing nutrients to the soil as they decay (Ellison and Gotelli 2002).

However, if spiders contribute nutrients to the decaying leaves, these nutrients may eventually be translocated into new pitchers. It is unknown if spiders do indeed contribute nutrients to *S. purpurea* during oviposition of senescing leaves. Their use by spiders presents no cost for the plant, and is therefore beneficial only to the spider.

The ecological relationship between *S. purpurea* and spiders can take many forms, each of which is determined by environmental, taxonomic, and individual factors. Although the taxon of spider involved in the interaction plays a critical part in determining which type of ecological relationship will result between the two organisms, environmental factors ultimately determine the taxa of spiders present in that location, and therefore which organisms will have the opportunity to interact. More detailed intricacies of this relationship may be revealed by uncovering individual characteristics of spiders, such as sex and maturity.

Although the relationship between spiders and *S. purpurea* is just one facet of the myriad of ecological interactions between the purple pitcher plant and its ecological community, its demonstrated complexity undoubtedly generates more questions than are answered here. Subsequently, future ecological studies of spiders and pitcher plants should follow up on the question of attraction versus retention; this concept may be also applied to the insect community to test my hypothesis that prey capture by pitcher plants is mostly one of prey retention rather than prey attraction. Other pitcher plants, such as *Sarracenia flava*, *Sarracenia leucophylla*, or *Sarracenia psittacina* may or may not be involved in similar relationships with spiders; researchers would do well to investigate the extent of this relationship with these plants and compare them to my own results. Finally, investigations into the ability of spiders, notably pisaurids, to escape being captured by pitchers may reveal unknown abilities in both organisms.

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# APPENDIX

## LIST OF CAPTURED SPIDERS

**Key**

- BEP: Blackwater Ecologic Preserve (VA); HBS: Highlands Biological Station (NC); JPP: Joseph Pines Preserve (VA). When these abbreviations follow a family heading, spiders identified to that family, but not further identified, were found at the specified location.
- "(?)" indicates that the identification is of questionable validity
- "*" indicates a probable new taxon

Agelenidae (BEP; HBS; JPP)

*Agelenopsis* sp. (BEP; HBS; JPP)

*Agelenopsis utahana* (HBS)

Anyphaenidae (BEP; HBS; JPP)

*Anyphaena celer* (BEP)

*Lupettiana mordax* (BEP)

Araneidae (BEP; HBS; JPP)

*Acacesia hamata* (JPP)

*Araneus* sp. (BEP)

*Gea heptagon* (HBS; JPP)

*Metepeira labryinthea* (HBS)

*Neoscona arabesca* (HBS)

Atypidae

*Sphodros atlanticus* (JPP)

Clubionidae (BEP; HBS)

*Clubiona catawba* (JPP)

*Clubiona rhododendri* (BEP; HBS)

Corinnidae (BEP; JPP)

*Castianeira longipalpus* (BEP)

*Phrurotimpus certus* (BEP)

*Scotinella madisonia* (JPP)

Ctenizidae

*Ummidia* sp. (BEP)

Cybaeidae (BEP)

Dictynidae (BEP; HBS)

*Cicurina arcuata* (BEP)

*Cicurina pallida* (BEP) (?)

*Dictyna* sp. (BEP)

*Lathys immaculata* (BEP)

Gnaphosidae (BEP; JPP)

*Callilepis pluto* (BEP)

*Cesonia bilineata* (BEP)

*Drassylus* sp. (JPP)*

*Gnaphosa fontinalis* (BEP)

*Haplodrassus signifer* (JPP)

*Micaria longipes* (BEP)

*Zelotes duplex* (BEP)

Hahniidae (JPP)

*Hahnia arizonica* (BEP) (?)

*Neoantistea agilis* (BEP; JPP)

Linyphiidae (BEP; HBS; JPP)

*Agyneta* sp. (BEP; HBS; JPP)*

*Agyneta serrata* (BEP)

*Bathyphantes crosbyi* (HBS) (?)

*Bathyphantes pallidus* (HBS)

*Centromerus cornupalpis* (HBS)

*Centromerus latidens* (BEP)

*Ceraticelus emertoni* (BEP)

*Ceraticelus formosus* (BEP) (?)

*Ceraticelus nesiotes* (BEP)

*Ceraticelus pygmaeus* (BEP)

*Ceraticelus similis* (HBS) (?)

*Ceratinella sphaerica* (BEP) (?)

*Ceratinops latus* (BEP) (?)

*Ceratinops rugosus* (BEP)

*Ceratinopsidis formosa* (BEP)

*Ceratinopsis interpres* (BEP)

*Ceratinopsis laticeps* (HBS)

*Ceratinopsis nigriceps* (BEP; JPP)

*Cheniseo sphagnicultor* (HBS)

*Eperigone entomologica* (HBS) (?)

*Eperigone maculata* (BEP; HBS; JPP)

*Eperigone serrata* (JPP)

*Eperigone tridentata* (HBS; JPP)

*Eperigone undulata* (JPP)

*Erigone autumnalis* (BEP; HBS; JPP)

*Erigone dentigera* (HBS)

*Florinda coccinea* (BEP; JPP)

*Frontinella pyramitela* (BEP; HBS)

*Grammonota gentilis* (HBS) (?)

*Grammonota gracilis* (HBS) (?)

*Grammonota inornata* (JPP)

*Grammonota maculata* (BEP)

*Grammonota trivittata* (JPP)

*Islandiana princeps* (BEP)

*Lepthyphantes sabulosa* (BEP)

*Microlinyphia mandibulata* (HBS)

*Neriene clathrata* (HBS; JPP)

*Neriene hammeni* (HBS) (?)

*Neriene obtusa* (HBS)

*Origanates rostratus* (BEP)

*Sisicottus montanus* (JPP) (?)

*Tapinopa bilineata* (BEP)

*Tutaibo anglicanus* (BEP)

(Unknown genus) sp. 1 (BEP)*

(Unknown genus) sp. 2 (BEP)*

*Walckenaeria* sp. (BEP)*

*Walckenaeria carolina* (BEP)

*Walckenaeria castanea* (BEP) (?)

*Walckenaeria digitata* (JPP)

*Walckenaeria pallida* (BEP)

*Walckenaeria spiralis* (HBS; JPP)

*Walckenaeria vigilax* (HBS) (?)

Liocranidae

*Agroeca* sp. (BEP)

Lycosidae (BEP; HBS; JPP)

*Allocosa funerea* (JPP)

*Gladicosa gulosa* (BEP)

*Gladicosa pulchra* (BEP)

*Hogna helluo* (BEP; JPP)

*Hogna punctulata* (BEP)

*Hogna rabida* (JPP)

*Pardosa milvina* (HBS; JPP)

*Pardosa saxatilis* (BEP; JPP)

*Pirata insularis* (BEP; HBS; JPP)

*Schizocosa duplex* (BEP)

*Schizocosa ocreata* (BEP)

*Trabeops aurantiacus* (BEP; JPP)

*Trebacosa marxi* (JPP)

*Trochosa* sp. (JPP) (?)

*Varacosa avara* (BEP; JPP)

Miturgidae (JPP)

*Strotarchus piscatorius* (BEP)

Mysmenidae (BEP)

*Microdipoena guttata* (BEP)

Oxyopidae (BEP; JPP)

*Oxyopes salticus* (BEP; HBS; JPP)

Pisauridae (BEP; HBS; JPP)

*Dolomedes* sp. (JPP)

*Pisaurina brevipes* (BEP; JPP)

Salticidae (BEP; HBS; JPP)

*Chinattus parvulus* (HBS)

*Eris marginata* (HBS)

*Eris militaris* (HBS)

*Habronattus coecatus* (BEP; JPP)

*Habronattus ocala* (BEP)

*Hentzia mitrata* (BEP; JPP)

*Lyssomanes viridis* (BEP)

*Maevia inclemens* (BEP; JPP)

*Maevia hobbsi* (JPP)

*Marpissa pikea* (JPP)

*Naphrys acerba* (BEP)

*Naphrys pulex* (BEP)

*Pelegrina galathea* (HBS)

*Pelegrina proterva* (BEP)

*Phidippus clarus* (JPP)

*Phidippus pius* (JPP)

*Phidippus princeps* (BEP; JPP)

*Phlegra hentzi* (BEP; JPP)

*Sarinda hentzi* (JPP)

*Sitticus cursor* (BEP)

*Sitticus magnus* (JPP)

*Synageles bishopi* (BEP)

*Thiodina puerpera* (BEP; JPP)

*Thiodina sylvana* (BEP)

*Tutelina elegans* (BEP; JPP)

*Tutelina hartii* (JPP)

*Zygoballus bettini* (BEP)

*Zygoballus nervosus* (BEP; HBS)

Tetragnathidae (BEP; HBS)

*Leucauge venusta* (BEP)

*Tetragnatha straminea* (HBS)

Theridiidae (BEP; HBS; JPP)

*Achaearanea globosa* (JPP)

*Enoplognatha caricis* (HBS)

*Episinus amoenus* (HBS)

*Phoroncidia americana* (BEP)

*Robertus frontata* (HBS)

*Spintharus flavidus* (BEP)

*Theridion albidum* (BEP; HBS)

*Theridion frondeum* (HBS)

*Theridion lyricum* (HBS)

Theridiosomatidae

*Theridiosoma gemmosum* (BEP)

Thomisidae (BEP; HBS; JPP)

*Coriarachne* sp. (HBS)

*Misumena vatia* (HBS)

*Misumenoides formosipes* (BEP; JPP)

*Misumenops oblongus* (HBS)

*Synema parvulum* (BEP)

*Tmarus* sp. (BEP; HBS; JPP)

*Xysticus ferox* (BEP) (?)

*Xysticus gulosus* (JPP)

## LIST OF CAPTURED HARVESTMEN (OPILIONES)

Opiliones (BEP; HBS; JPP)

*Hesperonemastoma kephati* (HBS)

*Leiobunum bimaculatum* (BEP; HBS)

*Leiobunum ventricosum* (HBS)

*Odiellus nubivagus* (HBS)

*Odiellus pictus* (HBS)

*Vonones sayii* (BEP)

# VITA

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**Biographical sketch**

Marc Milne received his BS in Biology from the University of North Florida in 2002 and began his PhD in Ecology at Old Dominion University in 2004. Marc then received his PhD in Ecology from Old Dominion University in 2010.

**Teaching background**

Bio 291 Ecology – Lecture; Bio 311 Genetics - Lecture and Lab; Bio 100/101 General Bio - Lecture and Lab (non-majors); Bio 292 Evolution – Lecture; Bio 115 General Bio - Lab (majors)

**Publications**

Milne, M. A., N. A. Grefe III, and D. A. Waller. 2008. Colonization and development of the Asian tiger mosquito (*Aedes albopictus*) in the purple pitcher plant (*Sarracenia purpurea*). American Midland Naturalist **160**:110-116.

Milne, M. A., V. R. Townsend Jr., P. A. Smelser, F. Smith, B. E. Felgenhauer, and M. K. Moore. 2009. Larval aquatic and terrestrial mites infesting a temperate assemblage of mosquitoes. Experimental and Applied Acarology **47**:19-33.

Milne, M. A., E. J. Ross, and D. E. Sonenshine. 2009. The attraction of *Triatoma dimidiata* and *Rhodnius prolixus* (Hemiptera: Reduviidae) to combinations of host cues tested at two distances. Journal of Medical Entomology **46**:1062-1073.