

Web Orientation and Prey Resources for Web-Building Spiders in Eastern Hemlock

RACHAEL E. MALLIS AND LYNNE K. RIESKE¹

University of Kentucky, Department of Entomology, S-225 Ag Science North, Lexington, KY 40546-0091

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ABSTRACT We examined the arthropod community on eastern hemlock, *Tsuga canadensis* (L.) Carr, in the context of its role in providing potential prey items for hemlock-associated web-weaving spiders. Using sticky traps simulating spider webs, we evaluated what prey items are available to web-weaving spiders in eastern hemlock based on web orientation (horizontal versus vertical) and cardinal direction. We found that the overwhelming majority (>70%) of prey items available to spiders in hemlock canopies were Diptera. Psocoptera, Hymenoptera, and Hemiptera comprised most of the remaining potential prey. A significant direction \times orientation interaction, and greater trap capture in some direction-orientation combinations, suggests that spiders might locate their webs in eastern hemlock canopies for thermoregulatory purposes, ultimately optimizing prey capture. We also evaluated these findings in the context of hemlock infestation by the invasive hemlock woolly adelgid, *Adelges tsugae* Annand. The adelgid is a sedentary insect with a mobile crawler stage that provides a readily available, easily obtained food source for predators in hemlock canopies. However, an abundance of alternative prey will affect within canopy spider distribution and the potential intensity with which spiders consume these prey. Understanding the response of spiders to potential prey availability is essential to understanding the trophic interactions involving these predators and their potential for influencing herbivore populations.

KEY WORDS web-weaving spiders, natural enemies, trophic interactions, predator-prey interactions, web location

Eastern hemlock, *Tsuga Canadensis* (L.) Carr, is a keystone species in eastern North America that regulates air and soil temperatures (Hadley 2000, Orwig et al. 2008), influences soil chemistry (Yorks et al. 2003, Lovett et al. 2004, Orwig et al. 2008) and stream characteristics (Collins et al. 2007, Hadley et al. 2008), and is responsible for the unique conditions found in riparian zones (Ford and Vose 2007, Hadley et al. 2008). Eastern hemlock provides food and habitat for game and nongame wildlife (Godman and Lancaster 1990, Ellison et al. 2005, Dilling et al. 2007), and also provides critical nesting habitat for songbirds, many of which are considered hemlock-dependent (Hooper 1978, Yamasaki et al. 2000, Ross et al. 2004). In the northeastern United States hemlocks occur in large contiguous stands across the landscape, while in the southern Appalachians their occurrence is more fragmented, and frequently confined to north-facing slopes, moist coves, riparian zones, and road cuts (Godman and Lancaster 1990, Ford and Vose 2007, Kincaid 2007, Kincaid and Parker 2008).

Within forests, microhabitat is a primary determinant of the occurrence of arthropods. In conifer canopies variables such as needle and twig density can

influence arthropod abundance (Halaj et al. 1998, Halaj et al. 2000), thereby affecting the composition and organization of arthropod community associates. Eastern hemlock canopies in the south-central Appalachians support an excess of 200 insect and 33 mite species, including 26 arthropod predators (Buck et al. 2005, Dilling et al. 2007, Turcotte 2008). However, dominant among arthropod predators are the spiders, which are the focus of our study.

Spiders are ubiquitous (Wise 1993) and are the most abundant arthropod group in tropical and temperate forest canopies (Halaj et al. 2000). Spiders are vital to food web dynamics, filling a wide range of spatial and temporal niches, and displaying an immense breadth of within-habitat taxonomic diversity. They demonstrate remarkable behavioral elasticity, and readily emigrate from, reoccupy, relocate to or take over web sites, and even form aggregations of webs (Higgins and McGuinness 1991). Habitat structure and prey abundance has been shown to play a role in the composition of spider communities within forest canopies (Mason et al. 1997, Halaj et al. 2000, Horváth et al. 2005). In canopies of European black pine, *Pinus nigra* Arnold, spider abundance, richness, and diversity increases with prey abundance and richness (Horváth et al. 2005). Depending on microhabitat and target prey,

¹ Corresponding author, e-mail: lrieske@uky.edu.

Table 1. Characteristics of study sites at Natural Bridge State Park and Pine Mountain State Park, KY

Site	Temp. (°C) ^a	Ppt. (cm) ^b	Plot	Elevation (m)	Aspect (°)	Slope (°)	Basal Area (m ² /ha)	HWA Infestation
Natural Bridge	12.6	10.3	1	271.9	38	5.5	1.26	None
			2	257.3	130	15.8	1.47	None
Pine Mountain	12.7	10.7	1	609.9	270	14.4	1.09	Mod.-High
			2	605.9	16	30.2	1.46	Low

^a Mean monthly temp (University of Kentucky College of Agriculture Weather Center).
^b Mean monthly precipitation (University of Kentucky College of Agriculture Weather Center).

many spiders orient their webs in a direction favorable for thermoregulation or prey capture (Biere and Uetz 1981, Caine and Hieber 1987, Higgins and McGuinness 1991, Bishop and Connolly 1992, Craig 1994, Ramirez et al. 2003, Justice et al. 2005). Some spiders are also prey specialists, favoring prey of specific taxa (Bradley 1993, Craig 1994, Nyffeler 1999). In addition to being taxon specific, prey preference may also be age specific based on instar size and the ability to take certain sizes and types of prey (Nyffeler 1999).

Currently little is known about the ecology of the spider community that resides in eastern hemlocks (but see Wallace and Hain 2000, Buck et al. 2005, Dilling et al. 2007, Turcotte 2008). A 2-yr census of hemlock spider associates yielded over 110 morphospecies from 20 families (R. E. Mallis, unpublished data), the most common of which were web-weaving Araneidae, Linyphiidae, and Tetragnathidae. Others collected included sit and wait predators, such as Thomisidae and Pisauridae, as well as active hunters, including Salticidae and Philodromidae.

We are examining the spider community on eastern hemlocks in the context of their ability to regulate arthropod herbivores. A variety of generalists and specialists, both native and non-native, exploit hemlock as a host plant (Rose and Lindquist 1994). Of particular concern in the eastern U.S. are the hemlock woolly adelgid, *Adelges tsugae*, and the elongate hemlock scale, *Fiorinia externa* Ferris. Both are of Asian origin (McClure 2002). The adelgid feeds on all hemlocks, but is particularly devastating to eastern hemlock, where infestations are often fatal (McClure 1989). Feeding by the adelgid causes needle drop, twig die-back and rapid tree death (Orwig et al. 2002). Since the mid 1980s the adelgid has established itself as a major pest of eastern hemlock forests in the eastern U.S. (McClure 1991, Butin et al. 2005). The elongate hemlock scale has a broader host range, but readily colonizes eastern hemlock; its interaction with the hemlock woolly adelgid on a given host plant accelerates host decline (McClure 2002). Although several arthropod predators occur in eastern hemlock canopies, these fail to effectively regulate populations of these exotic herbivores in the eastern U.S. (Wallace and Hain 2000).

Our focus has been to examine the composition of spider communities in eastern hemlock canopies and their relationship with the arthropod community, including the invasive hemlock woolly adelgid. Here we focus on what prey items are available to spiders in eastern hemlock canopies, and ask whether hemlock-

associated spiders might orient their webs to maximize prey capture.

Methods

Two 0.04 ha plots were established at 2 locations in the Eastern Coalfields region of Kentucky: Natural Bridge State Park (Powell Co.) and Pine Mountain State Park (Bell Co.) (Table 1). These plots had been established to evaluate successional changes associated with hemlock woolly adelgid (Spaulding and Rieske 2010). Natural Bridge State Park lies in the Eastern Knobs and is part of the Pottsville Escarpment. At the time our study was implemented the region was free of hemlock woolly adelgid. Pine Mountain State Park, situated on the south side of Pine Mountain, has been infested with hemlock woolly adelgid since 2006. Both locations lie in the Cumberland Plateau, where the terrain is characterized by steep slopes and ravines carved out of Pennsylvanian age coal-veined limestone, shale and sandstone (McDowell and Kentucky Geological Survey 1986). The eastern hemlock basal area was higher at our Natural Bridge site than our Pine Mountain site (Table 1). Site elevation and slope were greater at Pine Mountain than at Natural Bridge (Table 1). Three hemlocks in each plot (2 plots per site) were designated for trapping. Selected trees were 2.9–5.6 m in height, with diameters of 5–10 cm at 1.5 m above ground level.

To assess spider prey availability and determine whether web orientation affects prey capture, micro-site-specific sticky panels designed to simulate typical hemlock-associated spider webs were placed in hemlock trees. Sticky panels were constructed from three mil transparency film cut into 10 cm diameter discs (Harwood et al. 2001). Both sides were sprayed with a light coating of Tangle-Trap aerosol (The Tanglefoot Company, Grand Rapids, MI), creating a trap area of 162 cm² (81 cm² per side). Fishing line was used to secure sticky traps to selected branches. Traps were oriented vertically or horizontally, mimicking vertical and horizontal orb and sheet webs, and placed in perimeter branches at heights of 1.25–1.75 m in each cardinal direction. Thus each tree had a vertical and horizontal trap associated with it in each of the cardinal directions for a total of eight traps per tree. Pairs of traps were hung on two neighboring branches at a distance suitable to prevent interference between adjacent traps. Traps remained in place for 3 d, after which they were removed, wrapped in clear plastic film, taken back to the laboratory and stored at –20°C.

Table 2. Analysis of arthropod abundance, dipteran abundance, and ordinal richness on horizontally and vertically oriented sticky traps simulating spider webs

	Total abundance	Diptera	Ordinal richness
	χ^2/P	χ^2/P	F/P
Orientation	$\chi^2_1 = 0.35/0.55$	$\chi^2_1 = 0.75/0.39$	$F_{(1,77)} = 0.71/0.40$
Direction	$\chi^2_3 = 1.13/0.77$	$\chi^2_3 = 1.93/0.59$	$F_{(3,77)} = 0.24/0.87$
Direction*Orientation	$\chi^2_3 = 8.26/0.04$	$\chi^2_3 = 10.1/0.02$	$F_{(3,77)} = 0.63/0.60$
Site	$\chi^2_1 = 39.3/<0.0001$	$\chi^2_1 = 49.1/<0.0001$	$F_{(1,10)} = 4.72/0.06$
Plot (site)	$\chi^2_2 = 32.2/0.0001$	$\chi^2_2 = 31.6/<0.0001$	$F_{(1,10)} = 5.55/0.04$
Week	$\chi^2_9 = 71.6/0.0001$	$\chi^2_9 = 79.1/<0.0001$	N/A

Traps were placed in the same locations at each site over 10 separate sample intervals from 24 June to 12 September 2008, with 4 d between each 3 d sampling period. Thus there were 8 traps/tree \times 3 trees/plot \times 2 plots = 48 traps \times 3 d = 144 trap days at both Natural Bridge and Pine Mountain (10 replicates of 144 trap days at each site).

Traps were visually processed under a 40 \times dissecting microscope. The total number of arthropods per trap (spider, mite, insect) were counted and identified to the ordinal level (Triplehorn and Johnson 2005). Arthropod abundance and richness were calculated for trap orientation and direction.

Statistical Analysis. A generalized linear model (PROC GENMOD) with a Poisson distributed response was used. The model used site, plot nested within site, tree, sampling week, cardinal direction, and orientation (vertical versus horizontal). Response variables included total arthropod abundance and ordinal richness. Because of their numerical dominance we also included Diptera abundance as a separate response variable in the model. For the remaining response variables, including Hymenoptera, Psocoptera, Hemiptera, Coleoptera, Lepidoptera, Orthoptera, Acari, and Araneae abundance, generalized linear models with a dichotomized response (presence versus absence) were used. In these analyses, trap served as the experimental unit. We ran a second analysis using the same model, but with tree as the experimental unit and total abundance and dipteran abundance as the response variables. All analyses were performed using SAS 9.1 (SAS Institute 2006).

Results

There were 3,049 arthropods constituting potential prey items (0.5–15.0 mm) collected on the sticky traps over 10 wk of 3 d sample intervals. Eleven arthropod orders were represented, including Acari, Araneae,

Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Neuroptera, Orthoptera, Opiliones, and Psocoptera. Of these, the overwhelming majority were Diptera (71%), followed by Psocoptera (11%), Hymenoptera (7%), and Hemiptera (3%). A relatively small number of predominantly juvenile spiders were trapped (<2%). Most Diptera encountered were mosquitoes, gnats, and midges, while hymenopterans were comprised mostly of parasitoids (<4 mm).

There was a significant direction \times orientation interaction for total arthropod abundance and for total Diptera (Table 2). Neither direction nor orientation was significant for abundance individually, and there were no significant effects or interactions associated with ordinal richness. All possible pairwise comparisons of direction \times orientation were evaluated. Of the significant pairwise comparisons (Table 3), horizontal east-side traps were less likely to capture arthropods than were vertical east-side traps or horizontal west-side traps. Vertical east-side traps, vertical south-side traps, and horizontal west-side traps captured more potential prey than did vertical west-side traps (Table 3; Fig. 1).

There were significant effects of site for total abundance and dipteran abundance, and a weakly significant effect of site on ordinal richness (Table 2). There were fewer potential prey captured (both total prey and dipteran) at Natural Bridge (–HWA) than at Pine

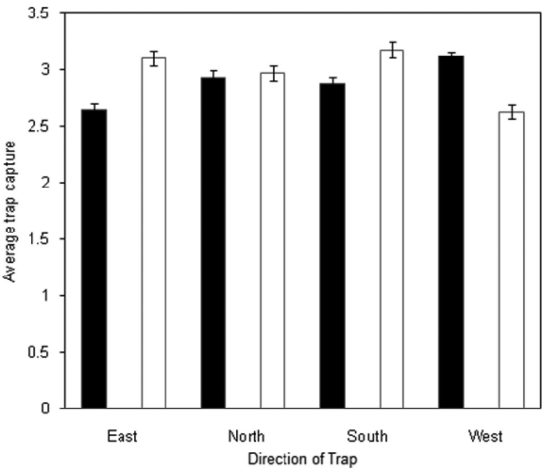


Fig. 1. Abundance (mean \pm SE per overall trap location) of prey items captured for each direction \times orientation combination (\square Vertical; \blacksquare Horizontal).

Table 3. Comparison of abundance of prey items captured based on direction and orientation of simulated spider webs located in eastern hemlock forests

Comparison	χ^2	P
Horizontal/East < Vertical/East	3.57	0.06
Horizontal/East < Horizontal/West	7.81	0.01
Vertical/East > Horizontal/West	3.3	0.07
Vertical/South > Vertical/West	4.12	0.04
Horizontal/West > Vertical/West	6.30	0.01

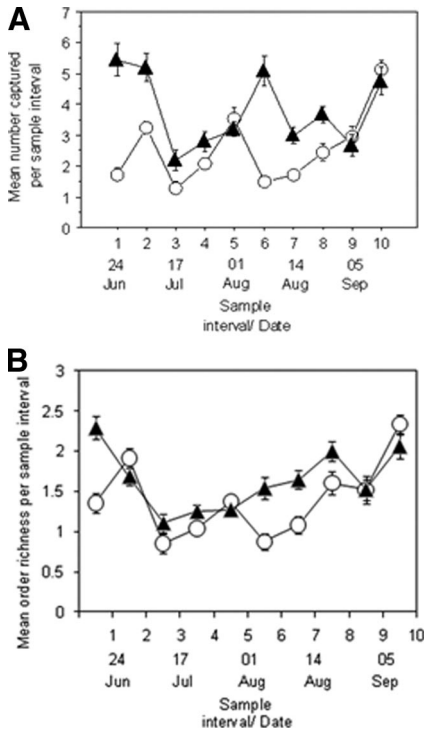


Fig. 2. A) Seasonal abundance (mean \pm SE per plot) of prey items captured in simulated spider webs placed in hemlock canopies in an uninfested forest (○: Natural Bridge) and an adelgid-infested forest (▲: Pine Mountain). (B) Ordinal richness (mean \pm SE per plot) of prey captured (○: Natural Bridge; ▲: Pine Mountain).

Mountain (+HWA) (1,227 versus 1,822 individuals) (Fig. 2A). There was a significant site(plot) effect for total abundance, dipteran abundance, and ordinal richness (Table 2), demonstrating the heterogeneity of our trap captures. At Natural Bridge (–HWA), both plots captured equivalent numbers of prey items, but at Pine Mountain (+HWA) prey capture differed between plots. Evaluating the data using tree as the experimental unit, a significant site effect emerges for total prey captured ($\chi^2_2 = 11.36$; $P = 0.007$), as well as the number of dipterans captured ($\chi^2_2 = 11.15$; $P = 0.008$). A similar analysis demonstrates a highly significant plot effect for total prey items ($\chi^2_2 = 11.90$; $P = 0.003$) and for Diptera ($\chi^2_2 = 11.76$; $P = 0.003$).

Total arthropod abundance and dipteran abundance were significantly affected by sample week, and temporal changes in abundance as well as ordinal richness were evident (Table 2; Fig. 2A and B). Both arthropod abundance and ordinal richness were lower at the Natural Bridge sites during trapping intervals 6–8 (7–12 August). There was a marginally significant interaction between sampling week and trap direction ($\chi^2_{27} = 38.6$, $P = 0.07$).

Discussion

Ours is the first study to evaluate seasonal prey availability for web-weaving spiders foraging in east-

ern hemlock. There were 8 insect and 3 noninsect arthropod orders present during the summer months (June–September), when we would expect the greatest prey abundance and diversity. Consistent with studies in other coniferous systems (Halaj et al. 2000, Horváth et al. 2005), Diptera were overwhelmingly the most abundant prey available, and the remaining prey were confined primarily to three other commonly occurring insect orders. In canopies of Douglas fir (*Pseudotsuga menziesii glauca* (Mayr) Franco), Diptera, Hymenoptera, and Psocoptera were the most abundant taxa captured in sticky traps, with dipterans comprising the majority (Halaj et al. 2000). Our approach and results are similar. However, when sampling bagged branch terminals, aphids (Homoptera) and Psocoptera were the most abundant arthropods encountered (Halaj et al. 1998, 2000). Similar trends were observed in red alder (*Alnus rubra* Bong.), western red cedar (*Thuja plicata* Donn ex D. Don), and noble fir (*Abies procera* Rehder) (Halaj et al. 1998), suggesting that sampling approach can bias results.

Prey availability is not necessarily indicative of prey consumption. In salt marshes with an evergreen understory and grasses, 29% of prey captured and consumed by *Argiope keyserlingi* Karsch was hymenopteran, but these comprised only 4% of potential prey available. In contrast, Diptera comprised 19% of the prey consumed, but 81% of prey items available (Bradley 1993). Hymenopterans and dipterans comprised 7 and 71%, respectively, of potential prey in our sampling, but it's difficult to predict whether a similar disproportionate consumption of prey occurs in eastern hemlock.

Prey availability does affect spider community composition and structure in some coniferous forest systems. During a western spruce budworm (*Choristoneura occidentalis* Freeman) outbreak, spider community structure shifted. Hunting spiders became more prevalent than web-builders, and species richness and diversity was higher for web-builders than hunting spiders (Mason et al. 1997). In black pine forests, increases in prey taxa richness and abundance were followed by increases in spider abundance, richness, and diversity (Horváth et al. 2005). In western hemlock, *T. heterophylla* (Rafinesque) Sargent, habitat structure and complexity was a significant predictor of spider abundance, richness and diversity, as well as prey abundance and richness (Halaj et al. 1998, 2000). Linyphiids and theridiids frequently occur on Douglas-fir and western hemlock, using needle bases as supports for their sheetwebs (Halaj et al. 1998, 2000). Araneidae, Linyphiidae, and Theridiidae are commonly found in our sampling in eastern hemlock canopies (R. E. Mallis, unpublished data).

The difference in prey abundance between plots at the adelgid-infested Pine Mountain site is worth noting. Radiant energy, sunlight penetration, wind speed and direction, and the understory component could contribute to potential prey distribution and abundance (Caine and Hieber 1987, Higgins and McGuinness 1991). Prey abundance was greatest in the plot with the lightest adelgid infestation (Table 1); this plot

had a less dense understory and greater sunlight penetration and wind exposure than its counterpart, and thus could harbor an increased number of flyways for potential prey such as Diptera and Hymenoptera.

The significant direction \times orientation interaction evident in our data demonstrates that the effects of orientation cannot be separated from direction with respect to prey capture. Some direction-orientation combinations were more likely to catch prey items than others (Fig. 1), suggesting that spiders may selectively locate their webs in hemlock canopies. Web orientation and morphology is highly variable in eastern hemlocks, as in other systems, and includes both horizontally and vertically oriented orb webs, cobwebs, triangle webs, mesh-webs, and sheetwebs (R. E. Mallis, personal observation). Spiders adjust the orientations of their webs for a number of reasons, including thermoregulation or to optimize prey capture (Biere and Uetz 1981, Caine and Hieber 1987, Bishop and Connolly 1992). In our study, east-side vertical traps and west-side horizontal traps captured the greatest number of prey. The differences in the east- and west-side pairwise comparisons suggest that spiders in eastern hemlocks are orienting their webs for thermoregulatory purposes (Fig. 1; Table 3), which in turn could also maximize prey capture.

This corroborates findings in other studies. In pine plantations the orb weaver, *Mangora gibberosa* Hentz, orients its web based on thermoregulation, which confers an advantage in prey capture because the spider warms up faster in the coolest part of the day (Caine and Hieber 1987). Web orientation and capture spiral composition affected prey interception rates of commonly occurring forest orb-weaving spiders in temperate deciduous forests (Opell et al. 2006). While vertically oriented webs had the highest rates of prey interception, the authors suggest that horizontal webs persist because smaller, horizontal orb-weaving spiders may be better able to fit their webs into more profitable locations than larger vertically oriented orb weavers in complex forest canopies (Opell et al. 2006). Within an oak (*Quercus* spp. L.) dominated deciduous forest, *Micrathena gracilis* Walckenaer oriented its web based upon thermoregulatory requirements (Biere and Uetz 1981); webs in the shade were oriented in a north/south direction, with the spider oriented in an east/west position; the opposite was found in open sites (Biere and Uetz 1981). This orientation behavior maximizes thermoregulation and allows for increased time spent on the web, thereby increasing prey availability (Biere and Uetz 1981). Both *Micrathena* and *Mangora* spp. are commonly encountered in eastern hemlock (R. E. Mallis, unpublished data). Similar results were observed for *Argiope* spp. in coastal scrub systems (Ramirez et al. 2003, Justice et al. 2005).

Web orientation is not always correlated with thermoregulation. In a tropical forest the tetragnathid orb weaver *Leucauge regnyi* Simon showed no correlation between web orientation or direction and thermoregulation. Horizontal and angled traps captured more prey than vertically oriented traps, and there was no difference in the number of prey captured by north/

south facing traps versus east/west facing traps, suggesting that webs were oriented to maximize prey encounters and not for thermoregulatory purposes (Bishop and Connolly 1992). However, that study used highly visible, white cheese cloth traps that may have influenced trap capture, whereas traps used in our study were transparent, with minimal visual cues to influence prey capture.

Similarly, studies in agroecosystems suggest that spiders may orient their webs to maximize prey capture (Harwood et al. 2005, Harwood and Obrycki 2007). Linyphiids in winter wheat appear to locate their webs in microsites with increased prey resources or are more open to flying/falling prey items (Harwood et al. 2001, 2003, 2004). In alfalfa, prey density did not drive web-site selection by ground-based erigones (Harwood and Obrycki 2007), but larger linyphiids showed a selective web-location strategy that was prey-driven: webs were constructed to increase chances of encountering higher quality dipteran prey items (Harwood and Obrycki 2007). Similarly, site conditions, including exposure to prey, affect the location and orientation of webs formed by *Nephila clavipes* (L.) in a scrub forest (Higgins and McGuinness 1991). Prey interception was also the dominant force directing web site selection of *Argiope argentata* (F.) in a grass clearing bordered by forests and a lake, where 50–90% of the prey captured was Hymenoptera (Craig 1994), far in excess of their composition in our study.

The ability to capture prey is influenced by spider foraging strategy, size, and age (Nyffeler 1999). Taxonomically diverse spiders will consume nonprey food items, including pollen and nectar, as well as honeydew from aphids and coccids (Patt and Pfannenstiel 2008, Wäckers et al. 2008). These are sedentary and periodically abundant food resources, similar to the hemlock woolly adelgid and elongate hemlock scale, which are sessile resources readily available in infested trees. While our traps did not capture any adelgid or scale crawlers, it is not unreasonable to suspect that spiders could consume these exotic herbivores. The extent to which the presence of these invasive species affects the structure and composition of spiders in eastern hemlock canopies is a focal point of future studies.

Invading hemlock herbivores lack biotic population regulators in the eastern U.S. Although the emphasis for hemlock woolly adelgid management has been on classical biological control, effective population regulation has not been the norm (Cheah et al. 2005, Grant 2008, McDonald et al. 2008, Paradis et al. 2008, Salom et al. 2008). Despite this, little attention has been given to endemic natural enemies. If spiders do consume adelgid they could also play a role in population regulation, by potentially augmenting classical biological control releases. In contrast, the potential for spiders to interfere with current biological control efforts by consuming the released beetles cannot be discounted. Our study adds another dimension to our understanding of the trophic interactions between spiders and their prey in eastern hemlock forests.

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