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Spiders (Araneae) inhabit lepidopteran-feeding shelters on ferns in Maine, USA

Daniel T. Jennings , Jerry R. Longcore , and James E. Bird

ABSTRACT

We sampled lepidopteran-feeding shelters on three species of ferns in Maine to determine use by spiders (Araneae). These feeding shelters were colonized by at least 39 species of spiders, representing 13 families and 33 genera. Most spider-inhabited shelters were on cinnamon fern (82.0%), with fewer on royal fern (12.8 %) and bracken fern (5.1%). Species richness was greater for web spinners (*n* = 26) than for hunters (*n* = 13). Abundance of individuals, however, favored hunters (*n* = 300) over web spinners (*n* = 186). Juvenile spiders (*n* = 410) were more frequent inhabitants than adult spiders (*n* = 78); females (*n* = 60) more frequent than males (*n* = 18). Shelters with single-spider occupants (*n* = 223) were more prevalent than shelters with multiple-spider occupants (*n* = 77). The proportion of shelters inhabited by spiders increased from June to mid–August, primarily through the addition of juveniles, and declined thereafter as the ferns senesced. Spider-habitation frequencies of shelters were similar each of the three study years (~ 35% of shelters occupied by spiders each year) despite unequal sample sizes between study sites and among fern species, and years (2012–2014). Spiders used lepidopteran-feeding shelters as refugia for molting and laying eggs, thus allowing spiders to conserve time, energy, and resources (silk).

RÉSUMÉ

Nous avons échantillonné des abris d'alimentation de lépidoptères sur trois espèces de fougères dans le Maine pour déterminer leur utilisation par les araignées (Araneae). Ces abris d'alimentation étaient colonisés par au moins 39 espèces d'araignées, représentant 13 familles et 33 genres. La majorité des abris occupés par des araignées étaient situés sur l'osmonde cannelle (82,0%), et un nombre moindre sur l'osmonde royale (12,8%) et la fougère-aigle (5,1%). La richesse spécifique était plus élevée chez les araignées tisseuses de toile (*n* = 26) que chez les araignées chasseuses (*n* = 13). Cependant, l'abondance des individus était plus élevée chez les chasseuses (*n* = 300) que chez les tisseuses de toile (*n* = 186). Les araignées juvéniles (*n* = 410) étaient plus fréquentes que les araignées adultes (*n* = 78); les femelles (*n* = 60) étaient plus fréquentes que les mâles (*n* = 18). Les abris occupés par une seule araignée (*n* = 223) étaient plus nombreux que ceux occupés par plusieurs araignées (*n* = 77). La proportion des abris occupés par des araignées a augmenté entre le mois de juin et la mi-août, surtout en raison d'une augmentation des juvéniles, puis a diminué par la suite, avec la sénescence des fougères. La fréquence d'occupation des abris par les araignées était similaire à chacune des trois années de l'étude (environ 35% des abris étaient occupés par des araignées chaque année), malgré un échantillonnage de taille différente entre les sites d'études, les espèces de fougères, et les années (de 2012 à 2014). Les araignées utilisaient les abris d'alimentation des lépidoptères comme refuge pour muer et pondre leurs œufs, ce qui leur permettait d'épargner du temps, de l'énergie et des ressources (soie).

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INTRODUCTION

Larvae of numerous species of Lepidoptera roll, fold, and tie leaves of their host plants to make protective shelters for feeding (Sigmon and Lill 2013). Ecologists and entomologists refer to habitat-modifying activities as ecosystem engineering by shelter makers and shelter users (Jones et al. 1994; Fukui 2001; Vieira and Romero 2013), terms that apply equally to spiders that modify leaves for retreats.

In addition to making their own retreat or shelter, some spiders inhabit shelters made by other arthropods, including shelters made by lepidopterous larvae that feed on plant leaves (Lill and Marquis 2007). Spiders that inhabit such shelters are considered secondary users or co-inhabitants because they are not the primary shelter maker (Fukui 2001; Lill and Marquis 2007). Most studies of shelter co-inhabitants concern those found on flowering plants such as trees and shrubs (reviewed by Fukui 2001). Occasionally spiders are listed among the co-inhabitants of these shelters, but their specific identities are seldom given. Even less is known about the co-inhabitants of leaf shelters found on non-flowering plants such as ferns. Studies of ferns generally address the identity of the insect shelter makers and shelter users, but seldom include information about the secondary users or co-inhabitants of these shelters.

On 7 July 2012, JRL found a small spider with an egg sac inside a rolled leaf shelter on cinnamon fern, *Osmunda cinnamomeum* (L.) C. Presi (Osmundaceae), at the Orono Bog Boardwalk (OBB) in Bangor, Penobscot County, Maine. Later, DTJ identified the female spider as *Ozyptila americana* Banks, 1895 (Thomisidae), a relatively uncommon crab spider in New England and Atlantic Canada (Dondale and Redner 1975; Dondale and Redner 1978; Kaston 1981; Paquin et al. 2010). After JRL's initial discovery we attempted to find additional specimens of *Ozyptila americana* on fern leaf shelters at the OBB and at one additional site in Penobscot County, i.e., the Caribou Bog (CB) in Old Town, ME. We soon discovered leaf shelters on other species of ferns, two different types of fern leaf shelters, a diversity of spider species occupuying these shelters, and seasonal differences in spider shelter habitation frequencies. Subsequently, we inventoried the spider fauna associated with leaf shelters on cinnamon fern, royal fern (*Osmunda regalis* L. (Osmundaceae)), and bracken fern (*Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae)).

METHODS

We collected lepidopteran feeding shelters on ferns at two sites: Site 1, along the OBB in Bangor, and adjoining habitats in the Rolland F. Perry (RFP) City Forest (~ 44° 51.969' N, 68° 43.739' W); and Site 2, the CB near Perch Pond (formerly Mud Pond) in Old Town (~ 44° 56.558' N, 68° 46.661' W). Site 1 is a mixed forest-bog with nearby wet drainages; Site 2 is a bog-heath-hemlock forest also with nearby wet drainages. Both sites were sampled each summer from 2012 to 2014. At Site 1, cinnamon ferns and royal ferns were found primarily in wet areas of the mixed forest-bog and its nearby drainages whereas bracken ferns were found in forest openings along trails, roadsides, and other cleared areas. At Site 2, cinnamon ferns were found in wet areas along the bog-forest interface and in nearby drainages leading to the bog. Bracken ferns at Site 2 grow chiefly along roadside openings. Royal ferns were absent in the areas we sampled at Site 2.

Collection of samples

At each study site, searches were made for insect feeding shelters on ferns by slowly walking through fern-inhabited areas of variable length and width. Shelters on cinnamon and royal fern were generally found near the frond apices; most were single per rachis, but occasionally doubles were found. Unlike the two *Osmunda* species, shelters on bracken usually occurred on branches below the apex of the frond blade.

To comply with site-conservation regulations at the OBB, searches were limited mostly to ferns reachable from the walkway. In the adjoining RFP City Forest, extensive areas northwest and southeast of the OBB entrance trail were searched. At CB, because of high water in the lagg (i.e., drainage corridor at the bog-woodland interface), searches were limited to fern-inhabited areas of the bog-woodland, plus wet areas extending into the adjacent hemlock forest. We also searched a few bracken ferns in open areas of the roadside-forest interface at CB. Sample sizes varied with regard to fern species composition and abundance at each site, apparent differences in shelter maker infestation rates among fern species, frequency of observer-site visitations (Site 1, $n = 19$ dates; Site 2, $n = 10$ dates), and differences in search durations (estimated range, 1.5–4.5 hours per site visit). Each shelter was carefully pinched off the frond rachis immediately below the shelter, and quickly placed individually in a pre-opened Ziploc® plastic bag (16.5 x 8.25 cm, or 17.7 x 12.7 cm). A penciled label with locality, date, and fern-species identification code was added to each bag.

Two basic types of insect feeding shelters were found; a round, ball-shaped or globe (G) shelter with the pinnae closely tied with silk (Fig. 1a) and, a curled-tied (CT) shelter with the pinnae tied near their bases, but with some apices free and extending at various angles (Fig. 1b). The latter resemble fiddleheads with a few unfurled pinnae.

Figure 1. Globe shelter on royal fern (a) constructed by lepidopterous larva of *Herpetogramma theseusalis* with pinnae closely tied with silk. Curled–tied shelter on cinnamon fern (b) constructed by lepidopterous larva *Olethreutes osmundana* with pinnae tied near bases, but apices extending outward. **Scale = 10 mm**.

Examination of samples

Field-collected samples were emptied onto white, brightly lighted paper toweling, and the bag interior examined for loose spiders and insects. The silk-tied pinnae were teased apart to expose the interior surfaces of each shelter. Spiders or insects attempting to escape were dabbed with an alcohol-dampened artist brush and placed in 1– or 2–dram vials containing 70% isopropyl alcohol. A penciled label with all field recorded data was added to each vial.

Spider identifications

DTJ examined all spiders submerged in 70% isopropyl alcohol under a Leica™ MZ-8 stereozoom microscope (10.1–80.0x magnification) equipped with fiber-optic lighting. Adult spiders were identified to species following the species descriptions and keys in the taxonomic literature; see Ubick et al. (2005) and literature cited therein. Most juvenile spiders were identified to family and genus except for two specimens (1 lost, 1 damaged). A juvenile of *Theridula* sp.and 12 juveniles of *Philodromus* (*rufus* group) sp. were determined to species based on their distinctive color patterns as illustrated by Levi (1954) and Dondale and Redner (1978), respectively. Because of insufficient characters, very small spiderlings (chiefly Erigoninae) were not determined beyond family or subfamily.

Spider nomenclature follows that of the World Spider Catalog, version 17.5 (2016); however, families and species are grouped by two basic foraging guilds (i.e., web spinner or hunter). The Linyphiidae are listed by subfamily per Draney and Buckle (2005). Representatives of all identified adult spiders have been deposited in the arachnid collections of the Museum of Comparative Zoology, Harvard University, Cambridge, MA.

Estimating faunal richness

Spider species determinations are based chiefly on characters and descriptions of the male and female genitalia, which are not fully developed until adulthood. Hence, most juvenile spiders could not be identified to species, which limits estimates of species richness (Jiménez–Valverde and Lobo 2006; Sackett et al. 2008). To help address this issue, we established the following conservative guidelines: a) each identified genus represents at least one species (e.g., *Frontinella* sp.), b) juveniles of identified adult species are assumed to belong to that species (e.g., *Tetragnatha* sp. and *Tetragnatha versicolor* Walckenaer, 1841 (Tetragnathidae)), and are not additive (i.e., 1 species not 2).

Data analyses

Because our collecting efforts were opportunistic and not standardized, non-parametric techniques were used to evaluate spider shelter habitation frequencies by study site (Magurran 1988), and by single *vs.* multiple occupancies (Sokal and Rohlf 1981). The Fisher Exact Test was used to examine the difference in proportions of curled-tied vs. globe shelters with spiders. The initial discovery of *Ozyptila americana* was included in the analyses.

RESULTS

Identities of shelter makers

The shelters from ferns yielded three species of Lepidoptera: *Lascoria ambigualis* (Walker) (Noctuidae) from royal fern; *Herpetogramma theseusalis* (Walker) (Crambidae) from cinnamon fern; and *Olethreutes osmundana* (Fernald) (Tortricidae) from shelters on cinnamon and royal ferns. The shelters on bracken were devoid of lepidopterous larvae, pupae, and moths; however, Gilligan et al. (2008) included this invasive fern among the host plants of *Olethreutes osmundana*.

Shelter collection sizes

Number of shelters collected varied by fern species, collection date, and study site (Table 1). Overall, we collected 1,074 shelters (Site 1, n = 751; Site 2, n = 323). Eighty-two percent (881 of 1,074) of the shelters came from cinnamon fern, the most common and frequently sampled fern at both study sites (Table 1). At Site 1, 138 of the shelters were found on royal ferns (12.8 %), a species not found at Site 2. Overall, only 55 of the shelters came from bracken ferns (5.1 %), both sites combined. June sample sizes ranged from 30–53 shelters per sample (mean ± SE = 38.3 ± 3.2, n = 6); July sample sizes ranged from 22–71 per sample (mean ± SE = 39.6 ± 4.5, n = 11); August sample sizes ranged from 19–61 per sample (mean ± SE = 37.1 ± 3.8, n = 11), with yearly totals shown in Table 1.

Frequencies of shelter types

More curled-tied shelters (1018 of 1074, 94.8%) than globe shelters (56 of 1074, (5.2%) were found each year (Table 1). Shelter types also differed among fern species each study year and over all years; collectively, cinnamon fern, n = 832 (CT), n = 49 (G); royal fern, n = 131 (CT), n = 7 (G); bracken fern, n = 55 (CT), n = 0 (G) (Table 1).

Spider habitation frequencies

Overall, the proportion of shelters inhabited by spiders was similar each year (i.e., in 2012, 30 of 84 (35.7%) shelters occupied; in 2013, 88 of 255 (34.5%) shelters occupied; and in 2014, 259 of 735 (35.2%) shelters occupied (Table 1). The proportion of shelters with spiders generally increased from early summer until mid–August, primarily through the addition of juveniles, and declined thereafter as the ferns began to senesce. In 2013, at Site 1, the mid-August proportion of shelters with spiders was 19 of 30 (63.3%) shelters occupied; thereafter 16 of 35 (45.7%) occupied. In 2014, at Site 1, the mid-August proportion of shelters with spiders was 23 of 50 (46.0%) shelters occupied; thereafter 20 of 48 (41.7%) shelters were occupied. In 2014, at Site 2, 24 of 40 (60.0%) shelters were occupied; thereafter 17 of 38 (44.7%) shelters were occupied. Overall the proportion of spiders in shelters was not different between curled-tied (35.5%, n = 1018) and globe shelters (28.6%, n = 56) shelters (Z_1 = -1.052, P = 0.293) (Table 1).

Table 1. Numbers of curled-tied and globe lepidopteran–feeding shelters inhabited by spiders per year, study site, and fern species during 2012–2014 in Maine, USA.

Year	Sites	Species of fern: Cinnamon		Royal		Bracken		Site Σ		% with spiders	
		CT	G	CT	G	CT	G	CT	G	CT	G
2012	1	17/42	2/5	2/11	0	0/1	0	19/54	2/5	35.2	40.0
	2	6/16	3/9	0	0	0	0	6/16	3/9	37.5	33.3
Yr Σ	1,2	23/58	5/14	2/11	0	0/1	0	25/70	5/14	35.7	35.7
2013	1	60/149	0/10	17/61	0	3/13	0	80/223	0/10	35.9	0.0
	2	8/22	0	0	0	0	0	8/22	0	36.4	0.0
Yr Σ	1,2	68/171	0/10	17/61	0	3/13	0	88/245	0/10	35.9	0.0
2014	1	135/350	4/11	21/59	1/7	7/32	0	226/441	5/18	37.0	27.8
	2	85/253	6/14	0	0	0/9	0	85/262	6/14	32.4	42.9
Yr Σ	1,2	220/603	10/25	21/59	1/7	7/41	0	248/703	11/32	35.3	34.4
2012-14	1	212/541	6/26	40/131	1/7	10/46	0	262/718	7/33	36.5	21.2
	2	99/291	9/23	0	0	0/9	0	99/300	9/23	33.0	39.1
Yr Σ	1,2	311/832	15/49	40/131	1/7	10/55	0	361/1018	16/56	35.5	28.6

NOTE: Study Site 1 = Orono Bog Boardwalk and adjoining Rolland F. Perry City Forest in Bangor; Site 2 = Caribou Bog near Perch Pond in Old Town. Fern species: Cinnamon fern, *Osmunda cinnamomeum* L.; Royal fern, *Osmunda regalis* L.; Bracken, *Pteridium aquilinum* (L.) Kuhn. Shelter type: CT = curled-tied; G = Globe.

Associated spider fauna

Collectively, at least 39 species of spiders, representing 13 families and 33 genera, inhabited lepidopteran-feeding shelters on ferns at our two study sites in east-central Maine (Table 2). Adult spiders represented 26 of the 39 species; two species were represented by identifiable juveniles (i.e., *Theridula emertoni* Levi, 1954 (Theridiidae) and *Philodromus placidus* Banks, 1892 (Philodromidae)). The 11 other species are provisional species, i.e., juveniles of genera that represent at least one species. Examples of provisional species include *Bathyphantes* sp., *Frontinella* sp., *Neriene* sp., *Pityohyphantes* sp., *Ghelna* sp., and *Pelegrina* sp. (Table 2).

The shelter inhabiting spiders represent two spider foraging guilds; web spinners (n = 26 species), and hunters (n = 13 species) (Table 2). Cinnamon ferns harbored the greatest diversity of families, genera, and species (13 families, 31 genera, and at least 36 species). This diversity is likely related to the prevalence of cinnamon ferns at both study sites, and the greater sampling frequency of this fern, i.e., overall, 82.0% of 1,074 shelters (Table 1). Quantitatively, the spider faunas inhabiting shelters on royal and bracken ferns were somewhat similar (7 families, 7 genera, and at least 8 species on royal fern; 7 families, 6 genera, and at least 7 species on bracken fern (Table 2). The total number of spider families on royal fern, however, includes an undetermined genus, species of Theridiidae. Only juveniles of undetermined and provisional species were shared in common among the shelters on these fern species, i.e., undetermined Linyphiidae (Erigoninae), *Emblyna* sp., *Clubiona* sp.,

Table 2. Spiders (Araneae) associated with lepidopteran feeding shelters on cinnamon (C), royal (R), and bracken (B) ferns in Penobscot County, Maine, USA.

Table 2 (cont'd)

		Number of spiders / fern species								
Spider taxa	**Site**	**Cinnamon**			**Royal**			**Bracken**		
		F	**M**	**j**	**F**	**M**	**j**	**F**	**M**	**j**
WEB SPINNERS										
THERIDIIDAE										
Enoplognatha ovata (Clerck, 1757)	1	1								
Neospintharus trigonum (Hentz, 1850)	1	1								
Theridion frondeum Hentz, 1850 *	1	3	1							
Theridion glaucescens Becker, 1879	1		1							
Theridion sp.	1,2			9						
Theridula emertoni Levi, 1954	1									1
Thymoites unimaculatus (Emerton, 1882) *	1	1								
Undetermined genus, species	1			1			2			
LINYPHIIDAE, Linyphiinae										
Bathyphantes sp.	1,2			3						
Frontinella sp.	1			1						
Helophora insignis (Blackwall, 1841)	1	1								
Neriene sp.	1			1						
Pityohyphantes sp.	1,2			6						
Undetermined genus, species	1			4						
LINYPHIIDAE, Erigoninae										
Ceraticelus fissiceps (O. P-Cambridge, 1874)	1,2	12	2							
Ceraticelus sp.	1			3						
Dismodicus decemoculatus (Emerton, 1882)	1,2	1			1					
Grammonota ornata (O. P-Cambridge, 1875)	1	1								
Phlattothrata flagellata (Emerton, 1911)	2	1								
Tapinocyba prima Dupérré & Paquin, 2005	2	1								
Undetermined genus, species	1,2			20			5			1
TETRAGNATHIDAE										
Pachygnatha dorothea McCook, 1894	1	1								
Pachygnatha sp.	1			1						
Tetragnatha versicolor Walckenaer, 1841	1	2	1							
Tetragnatha sp.	1,2			7						
ARANEIDAE										
Araneus corticarius (Emerton, 1884)	1					1				
Araneus sp.	1			2						
Neoscona sp.	1						1			
Undetermined genus, species	1						1			
AGELENIDAE										
Agelenopsis potteri (Blackwall, 1846)	1	2								
Agelenopsis utahana (Chamberlin & Ivie, 1933)	2		1							
Agelenopsis sp.	1			1						
DICTYNIDAE										
Emblyna annulipes (Blackwall, 1846)	1	1	1							
Emblyna phylax (Gertsch & Ivie, 1936) *	1	1								
Emblyna sublata (Hentz, 1850)	1,2	2								
Emblyna sp.	1,2			71			2			1
AMAUROBIIDAE										
Callobius sp.	1			1						
Web spinner subtotals:		32	7	131	1	1	11			3
HUNTERS										
PISAURIDAE										
Pisaurina sp.	1			1						
CLUBIONIDAE										
Clubiona bishopi Edwards, 1958 *	1,2	11	4		7	1				
Clubiona maritima L. Koch, 1867	1				1					
Clubiona sp.	1,2			141			28			5
GNAPHOSIDAE										
Drassyllus sp.	2			2						
Haplodrassus hiemalis (Emerton, 1909)	1	1								
PHILODROMIDAE										
Philodromus placidus Banks, 1892	1,2			11						1
Philodromus rufus vibrans Dondale, 1964	2	1								
Philodromus sp. (*rufus* group)	1,2			3			1			1
THOMISIDAE										
Ozyptila americana Banks, 1895 *	1	1								
Xysticus sp.	1,2			7						2

Table 2 (cont'd)

		Number of spiders / fern species								
Spider taxa	**Site**	**Cinnamon**			**Royal**			**Bracken**		
		F	M	j	F	M	j	F	M	j
SALTICIDAE										
Eris militaris (Hentz, 1845)	1,2	4	5							
Eris sp.	1,2			30			3			1
Evarcha hoyi (Peckham & Peckham, 1883)	1	1								
Evarcha sp.	1			1						
Ghelna sp	1,2			4						
Pelegrina sp.	1,2			19						
Undetermined genus, sp.	1,2			2						
Hunter subtotals:		19	9	221	8	1	32			10
UNDETERMINED	2			2						
Overall totals:		51	16	354	9	2	43			13

Note: Spider taxa are listed by spider–foraging guild (web spinners, hunters). Species with female guarding an egg sac = *, F = female, M = male, j = juvenile. Study Site 1 = Orono Bog Boardwalk. Site 2 = Caribou Bog.

Philodromus sp. (*rufus* group), and *Eris* sp. (Table 2).

Sørensen's qualitative measure of similarity (Magurran 1988) indicates that the spider fauna inhabiting shelters at the study sites were dissimilar ($Q_S = 41.5$, $P < 0.5$). This dissimilarity is related to the number of species ($n = 23$) inhabiting shelters at Site 1, but not at Site 2. In contrast, shelters at Site 2 yielded only 5 species of spiders not found among the shelters at Site 1 (i.e., *Phlattothrata flagellata* (Emerton, 1911) (Linyphiidae), *Tapinocyba prima* Duperre & Paquin, 2005 (Linyphiidae), *Agelenopsis utahana* (Chamberlin & Ivie, 1933) (Agelenidae), *Drassyllus* sp., and *Philodromus rufus vibrans* Dondale, 1964 (Philodromidae), Table 2). These five species were present in shelters on cinnamon ferns at Site 2. The remaining 11 species (*Bathyphantes*, sp., *Pityohyphantes* sp., *Ceraticelus fissiceps* (O.P.-Cambridge, 1894) (Linyphiidae), *Dismodicus decemoculatus (*Emerton, 1882) (Linyphiidae), *Emblyna sublata* (Hentz, 1850) (Dictynidae), *Clubiona bishopi* Edwards, 1958 (Clubionidae), *Philodromus placidus*, *Xysticus* sp., *Eris militaris* (Hentz, 1845) (Salticidae), *Ghelna* sp., and *Pelegrina* sp.) were present in cinnamon fern leaf shelters at both study sites (Table 2). As Sørensen's qualitative measure of similarity does not account for species abundances (Magurran 1988), the coefficient of similarity was calculated based on Sørensen's quantitative (i.e., number of individuals of all species) measure of similarity, ($Q_N = 42.2$, $P < 0.5$) also indicating that the sites were dissimilar.

Most of the shelter inhabiting species were associated with leaf shelters on cinnamon ferns at both sites (Table 2). Three species (*Araneus corticarius (*Emerton, 1884*)*, (Araneidae), *Neoscona* sp., and *Clubiona maritima* L. Koch, 1867 (Clubionidae)) were found exclusively in shelters on royal ferns; however, *Dismodicus decemoculatus* and *Clubiona bishopi* were found in shelters on both cinnamon and royal ferns. A juvenile of *Theridula emertoni* was found only on bracken fern. Representatives of only four species (*Emblyna* sp., *Clubiona* sp., *Philodromus* sp. (*rufus* group), and *Eris* sp.) were found in shelters on all three species of ferns.

Spider numbers, life stages, and adult sex ratios

Over all sampling dates, study sites, and fern species in east-central Maine, spiders that actively hunt for prey were more prevalent (300 of 486, 61.7%) among these shelters than spiders that use webs for capturing prey (186 of 486, 38.3%). We were unable to determine the foraging guild for two juveniles (1 lost, 1 damaged), which yielded a total of 488 spiders (Table 2). Most shelter inhabiting spiders (421 of 488, 86.3%) came from cinnamon fern, the most common and frequently sampled fern (Table 2). Royal ferns accounted for (54 of 488, 11.1%) of the spiders, and bracken ferns accounted for (13 of 488, 2.7%) of the spiders. Juvenile spiders were more common (84.0%) occupants of shelters than adults (16.0%). Female spiders were more common 76.9% than males 23.1%, $n = 78$ adults. The Clubionidae ranked first in terms of total individuals, i.e., 24 adults and 174 juveniles of *Clubiona*, in fern–leaf shelters (Table 2). The Dictynidae ranked second with 5 adults and 74 juveniles of *Emblyna*; the Salticidae third with 10 adults and 60 juveniles, chiefly *Eris* sp. and *Pelegrina* sp.; the Linyphiidae fourth with 20 adults and 44 juveniles (Table 2). All other families were represented by fewer than 25 individuals each.

Nesting female spiders

Five species of spiders nested in fern leaf shelters, all at Site 1 (i.e., *Theridion frondeum* Hentz, 1850 (Theridiidae), *Thymoites unimaculatus* (Emerton, 1882) (Theridiidae), *Emblyna phylax* (Gertsch & Ivie, 1936) (Dictynidae), *Clubiona bishopi*, and *Ozyptila americana*). Four of the five species guarded egg sacs during July; females of *Clubiona bishopi* guarded egg sacs during both July and August, and a female *Emblyna phylax* guarded three overlapping egg sacs in August. Eight of 11 nesting females inhabited lepidopteran-feeding shelters on cinnamon ferns at Site 1. Three females of *Clubiona bishopi*, each with an egg sac, occupied shelters on royal ferns at Site 1. Two of the three *Clubiona bishopi* females guarded egg sacs within the confines of the same shelter on a royal fern. Female spiders favored curled-tied shelters (10 of 11, 90.9%) as nesting havens compared to globe shelters (1 of 11, 9.1%).

Single *vs.* multiple spider occupants

Shelters with a single spider were more common (*n* = 289) than shelters with multiple spiders (*n* = 88); a consistent trend each study year with single occupancies ranging from 70–78% during 2012–2014. For all study years and fern species combined, the mean (± SE) of single-spider occupancies was greater (74.3 ± 2.3%) than that of multiple-spider occupancies (25.7 ± 2.3%); G–test $_{1\ df.}$ = 112.9, $P \leq 0.001$. Among shelters with single spiders, hunters (61.2%) were more common than web spinners (38.8%). Juveniles of *Clubiona* and *Eris*, and female *Clubiona bishopi* were common among shelters occupied by single hunters; juveniles of *Emblyna* and female *Ceraticelus fissiceps* were common among shelters with single web spinners (Table 2). Shelters with multiple spiders ranged from two to four individuals per shelter, with the following categories represented: all web spinners (*n* = 15), all hunters (*n* = 38), or both foraging guilds (*n* = 35). Overall, hunters were by far the most prevalent among shelters with multiple spider occupants.

Shelters with multiple spiders also represented a diversity of life stages and taxa. Examples included: male-juvenile, *same* taxa (*Theridion frondeum* ♂, *Theridion* sp. juv.); male-juvenile, *mixed* taxa (*Eris militaris* ♂, *Clubiona* sp. juv.); female-juvenile, *same* taxa (*Emblyna phylax* ♀, *Emblyna* sp. juv.); female-juvenile, *mixed* taxa (*Grammonota ornata* ♀, *Clubiona* sp. juv.); female-female, *same* taxa (*Clubiona bishopi* ♀, *Clubiona bishopi* ♀); and female-male, *mixed* taxa (*Tetragnatha versicolor* ♀, *Clubiona bishopi* ♂). Life stages and taxa were even more complex among triple and quadruple occupancies; however, no male–male occupancies were found. Single and multiple spiders were found inhabiting shelters on all three species of ferns. The shelter association frequencies were: cinnamon fern, *n* = 250 singles *cf. n* = 76 multiples; royal fern, *n* = 32 singles *cf. n* = 9 multiples; bracken fern, *n* = 7 singles *cf. n* = 3 multiples. All categories of spider-shelter habitations (singles, doubles, triples, quadruples) were found on cinnamon and royal ferns at study sites. These shelter habitations, however, were in descending order, i.e., singles were more common than doubles, doubles more common than triples, etc. Multiple occupant shelters on bracken seem to be limited to two individual spiders (e.g., *Clubiona* juv., *Xysticus* juv.), possibly because shelters on this invasive plant are smaller than those on cinnamon and royal ferns.

Other arthropods inhabited fern leaf shelters at the study sites, including mites (Acari), springtails (Collembola), psocids (Corrodentia), bugs (Hemiptera), moth larvae and pupae (Lepidoptera), beetles (Coleoptera), ants and wasps (Hymenoptera), flies (Diptera), and snails (Gastropoda). Most of these non–spider co–inhabitants were associated with shelters on cinnamon ferns.

DISCUSSION

This exploratory study demonstrates that spiders frequently inhabit leaf shelters made by lepidopterous larvae on three species of ferns in Maine. The proportions of shelters occupied by spiders are fairly consistent (~ 35%), despite unequal sample sizes during the three years. These habitation frequencies are comparable to those found by other investigators. In northern Québec, Cappuccino (1993) noted that spiders comprise 25% of the secondary occupants in leaf shelters made by the birch tubemaker, *Acrobasis betulella* Hulst. (Lepidoptera: Pyralidae). She concluded that spiders are more likely to be present in leaf shelters than on adjacent paper birch (*Betula papyrifera* Marsh.) foliage. In lepidopteran rolled alder (*Alnus* spp.) leaves of Washington's Cascade Range, Miliczky et al. (2014) found spider shelter occupancies ranging from 15–44%.

Differences among fern species most likely reflect different levels of infestation by shelter making lepidopterans, i.e., larvae of *Olethreutes osmundana* make curled-tied shelters whereas larvae of *Herpetogramma theseusalis* make globe shelters. The globe shelters encountered in Maine are made by larvae of *Herpetogramma theseusalis* and are similar to those described and illustrated by Ruehlmann et al. (1988) for *Herpetogramma aeglealis* (Walker), a species that feeds on Christmas fern (*Polystichum acrostichoides* (Michx.)) in Georgia. In southern coastal Maine, LoPresti and Morse (2013) also found *Herpetogramma theseusalis* in leaf shelters on sensitive fern (*Onoclea sensibilis* L.).

In their review of the Olethreutine moths of the Midwestern United States, Gilligan et al. (2008) noted that larvae of *Olethreutes osmundana* construct shelters by folding and tying adjacent leaves (pinnae) of ferns. Such shelters are distinctly different from globe shelters; hence, we coined the term curled-tied shelter, which refers to its resemblance of a late stage fiddlehead, i.e., an apically expanded crozier with basal pinnae silk-tied. Gilligan et al. (2008) included Maine in the distribution of *Olethreutes* *osmundana* and noted that the larvae of this moth feed on all three species of ferns sampled during this study.

The differences in shelter type (globe *vs* curled-tied) and abundance of each type possibly reflect different levels of infestation by shelter making lepidopterans. Curled-tied shelters were more common than globe shelters at both sites. We suspect that *Lascoria ambigualis*, the third species of lepidopteran associated with fern shelters during this study, is a visitor to shelters rather than a shelter maker. The recorded plant hosts of *Lascoria ambigualis* include *Chrysanthemum*, ragweed, and horseradish (Beadle and Leckie 2012).

The spiders found inhabiting fern leaf shelters represent diverse taxa, (i.e., 13 families, 33 genera, and at least 39 species). By comparison, Miliczky et al. (2014) reported spiders of 9 families, 13 genera, and at least 17 species in rolled alder (*Alnus* spp.) leaves of the Cascade Range in Washington State. Numerous other studies of leaf shelter co-inhabitants, chiefly on broadleaf trees, list even fewer families and species of spiders or simply spiders; see review by Fukui (2001) and literature cited therein. In southern coastal Maine, LoPresti and Morse (2013) included the names of two spider families (Thomisidae and Salticidae) among the inhabitants of lepidopteran shelters on sensitive fern.

Not surprisingly, spider foraging guild representation among shelter inhabitants favored web-spinner species over hunter species, a trend found elsewhere in New England (Kaston 1981) and Atlantic Canada (Pickavance and Dondale 2005; Paquin et al. 2010). In Washington State, Miliczky et al. (2014) found more species of web spinners than hunters inhabiting lepidopteran-rolled alder leaves. In our study, however, the fern leaf shelters harbored more individual hunters (61.7%), especially Clubionidae than web spinners (38.3%). In Canada, Morris (1972) concluded that the Clubionidae was the most common family of spiders inhabiting colonial nests of the fall webworm (*Hyphantria cunea* Drury). The most prevalent mature spiders in webworm nests were *Clubiona canadensis* Emerton, 1890; *Clubiona moesta* Banks, 1896; and *Clubiona obesa* Hentz, 1847. In Washington State, Miliczky et al. (2014) also found hunters, especially individuals of *Clubiona pacifica* Banks, 1896 and *Clubiona* sp., to be more common than web spinners.

Female spiders favored curled-tied shelters most likely because of their overwhelming abundance compared with globe shelters at study sites. Shelter architecture and available interior space may influence nesting-site usage by spiders. Globe shelters have less interior space than curled-tied shelters after frass accumulates from the shelter maker, i.e., *Herpetogramma theseusalis* larva.

Despite extensive literature searches, we found only limited information about the nesting habitats of the five species of spiders with egg sacs in fern leaf shelters. Only one of the five has been recorded as an occupant of leaf shelters made by lepidopterans, i.e., Miliczky et al. (2014) included *Emblyna phylax* among the spiders found nesting in lepidopteran-rolled alder leaves. Although capable of spinning their own self-made shelter, our study provides evidence that all five species are also secondary users of existing fern-leaf shelters made by lepidopterans. Most likely none of the five species are restricted to such shelters; however, a nesting site preference may be involved. We suspect that *Clubiona bishopi*, the species found most frequently with egg sacs, is an opportunistic nester that takes advantage of an existing shelter rather than constructing one of its own. This clubionid was not found in self-made folded leaf shelters on ferns or other plants.

Fern leaf shelters are refugia for spiders to molt, nest, and rear their young. Spiders are most susceptible and vulnerable to attack by natural enemies during molting when they are somewhat defenseless (Gertsch 1979; Fink 1987; Foelix 2011). Despite their protective silk coverings, spider eggs are susceptible to attack by numerous dipterous and hymenopterous parasitoids, and by scavenging ants, beetles, and other spiders (Evans 1969; Austin 1985; Hieber 1992). Shelters with insect co-inhabitants are potential sources of prey for spiders. Small insects, such as springtails and psocids, serve as prey for juvenile spiderlings; large insects, including lepidopteran shelter makers, serve as prey for adult spiders (Damman 1987; Miliczky and Calkins 2002). Spiders also feed on other spiders, a behavior possibly contributing to the preponderance of single-spider occupancies compared to multiple occupancies. Shelters with multiple spiders frequently included: females with their offspring (e.g., *Emblyna phylax* ♀, *Emblyna* juv., *Emblyna* juv.), and juveniles of the same taxa (e.g., *Clubiona* juv, *Clubiona* juv.). Adults and juveniles of mixed taxa (e.g., *Emblyna* juv., *Pelegrina* juv.) were less frequent occupants. Other studies have shown that lepidopteran leaf shelters provide some protection from the elements for their occupants (Lill and Marquis (2007). Spiders may conserve time, energy, and resources (silk) by occupying shelters made by others.

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