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Spider use of caterpillar shelters

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Abstract. Although caterpillars commonly construct shelters on vegetation that other species subsequently occupy, few studies have focused on the spiders that often recruit to them. Fern moth larvae *Herpetogramma theseusalis* (Lepidoptera: Crambidae) produce large, roughly circular shelters on ferns that provide them with food and protection. Female jumping spiders *Phidippus clarus* Keyserling, 1885 (Salticidae) with brood or first-instar young made up over two-thirds of the spiders tallied in a study of abandoned fern moth shelters. The only other species tending young, the sac spider *Clubiona bishopi* Edwards, 1958 (Clubionidae), made up less than 10% of the total. Only eight species of spiders used these shelters, one-half to one-fourth that of three other studies and differing in the prevalence of jumping spiders, as opposed to a prevalence of sac spiders in the other studies. Although fern moth shelters provide important nest sites for two spiders, these sites did not enhance diversity of the spider community.

Keywords: *Phidippus clarus*, *Clubiona bishopi*, fern, fern moth

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Caterpillars of many foliage-feeding moths and butterflies build shelters on their food source that a wide variety of small invertebrates subsequently exploit (Fukui 2001; Nakamura & Ohgushi 2003; Miliczky et al. 2014). However, although spiders are among the commonest secondary inhabitants of these sites (Cappuccino 1993; Miliczky et al. 2014; Jennings et al. 2017), relatively few studies of these shelters provide detailed information on them (Jennings et al. 2017).

These shelters provide their secondary inhabitants with several possible benefits, which may differ, with the occupant providing a possible food source as well as protection from predators, weather and desiccation (Fukui 2001; Lill & Marquis 2007; LoPresti & Morse 2013). Shelters vary greatly in their complexity, from simple ties that merely adhere two leaves to each other with a few strands of silk (Lill & Marquis 2003), to complex structures that provide considerable internal space. Indeed, these shelter-makers qualify as ecosystem engineers: they may modify a habitat in such a way as to enhance or facilitate its use by others (Jones et al. 1994; Lill & Marquis 2003).

Given the scarcity of information about spiders in shelters, the purpose of this study was to investigate the secondary occupants of shelters constructed on ferns by caterpillars of a moth species, especially the spiders inhabiting them. Recognizing that such sites may play an important role in biodiversity (e.g., Martinsen et al. 2000), I also wished to establish whether the shelters contributed to the diversity of spiders in this habitat. Additionally, I wished to compare these results against the small number of studies covering similar situations, looking for resemblances and differences and the possible bases for them.

Larvae (caterpillars) of the fern moth *Herpetogramma theseusalis* (Lepidoptera: Crambidae) construct complex shelters from the terminal pinnae of ferns by rolling them into ball-shaped structures, into which the caterpillars position themselves, thereby gaining both food and protection (Morse 2009, 2011). The caterpillars subsequently pupate in their shelters, eclose and leave these sites in July and early August, at which point secondary inhabitants, including spiders, sow bugs, collembolans, mites, ants, parasitoid wasps, beetles and flies, begin to occupy them. Fern moth caterpillars build their shelters on several species of ferns (D.H. Morse, unpubl. data), but constructed the shelters reported here on sensitive fern *Onoclea sensibilis* (Dryopteridaceae) and marsh fern *Thelypteris palustris* (Thelypteraceae) growing in a seasonally moist site of approximately 0.3 ha formed by two intermittent streams in an old field in South Bristol, Lincoln Co., Maine USA (43°57′N, 69°33′W). Approximately three-fourths of the study site consisted of sensitive ferns, with the remainder made up by marsh ferns.

Sterile fronds of sensitive ferns in the study area averaged 60 cm in height and 25 cm at maximum breadth; marsh ferns averaged 45 cm in height and 15 cm at maximum breadth. The shelters varied considerably in abundance, in extreme instances reaching numbers of up to 100/m^2 (Bar-Yam & Morse 2011), though this density far exceeded that in most of the habitat (D.H. Morse, pers. observ.). The shelters varied from 1.5 to 4 cm in diameter, depending on the size of the caterpillar and the number of days it had occupied the structure. By late August, most of the shelters had senesced and dried, only containing occasional remaining bits of living fern tissue. As a result, they provided little food for young fern moth caterpillars – many had already departed (Morse & Chapman 2015). This evacuation greatly decreased the amount of food available for spiders or other small carnivorous invertebrates occupying these shelters. Perhaps as a result, I failed to find several species reported in other studies of similar shelters.

Each year (2002–2018), I haphazardly collected up to 15 shelters in several parts of the study area at the end of the growing season (late August and early September). At times I could not find a full set of 15 shelters, and after several years, some sites ceased to yield any shelters. I placed the collected shelters in plastic bags for return to the laboratory, dissected them within a few hours and recorded their contents.

I compared the spiders' occupation of sensitive and marsh ferns with G tests for independence and the comparison of numbers of species in the different studies with G tests for goodness of fit.

Table 1.—Contents of shelters constructed by fern moths *Herpetogramma theseusalis* (Lepidoptera: Crambidae) on sensitive and marsh ferns (*Onoclea sensibilis* and *Thelypteris palustris*). Other* = Parasitoid wasps and flies, detritus-feeding flies, ants, beetles, bugs, collembola, mites, sow bugs.

Content	Sensitive fern	Marsh fern	% of total (combined)
Empty	883	282	36.9
Remains of moth or wasp only	856	236	34.5
Caterpillars	321	76	12.5
Spiders	311	45	11.2
Other*	146	10	4.9
Total	2517	649	100.0

Table 2.—Spiders found in shelters constructed by fern moths *Herpetogramma theseusalis* (Lepidoptera: Crambidae) on sensitive and marsh ferns (*Onoclea sensibilis* and *Thelypteris palustris*). * = Includes some immatures tentatively assigned to this species.

Species	Sensitive fern	Marsh fern	% of total (combined)
Phidippus clarus Keyserling, 1885	217	29	69.0
Pelegrina insignis (Banks, 1892)*	48	12	16.9
Clubiona bishopi Edwards, 1958*	29	2	8.7
Xysticus emertoni Keyserling, 1880	12	2	3.9
Enoplognatha ovata (Clerck, 1757)	2	0	0.6
Araneus trifolium (Hentz, 1847)	1	0	0.3
Pardosa moesta Banks, 1892	1	0	0.3
Misumena vatia (Clerck, 1757)	1	0	0.3
Total	311	45	100.0

Over the years of 2002–2018, I examined 3,156 shelters, the majority of which contained no living individuals (Table 1). The largest single category of shelters contained no signs of past inhabitants, but large numbers contained signs of either fern moths or their extremely common parasitoid, the braconid wasp *Alabagrus texanus* (Brachonidae) (Morse 2011) (Table 1). Most of these remains consisted of pupal cases, but 21.7% of the fern moth remains and 15.9% of the wasp remains consisted of individuals that failed to emerge. First- or second-instar fern moth caterpillars born in the shelters made up the largest single group of live animals (Table 1). I have separated the caterpillars from other inhabitants of the shelters in this analysis (Table 1), because they were, in a sense, primary inhabitants, their parents having laid eggs within the shelters (Morse 2017).

Spiders (Table 2) made up by far the largest proportion of secondary inhabitants (Table 1) and had probably consumed additional caterpillars as well, which due to their small size, would have provided easy prey for many of the spiders. I obtained 356 spiders of eight or more species. The jumping spider *Phidippus clarus* Keyserling, 1885 (Salticidae), an abundant species in the study area, dominated the numbers; nearly all were females tending either eggs or first-instar brood. (I did not include the early instars attended by their parents in the count of individuals.) Many other *P. clarus* near the study area constructed their own shelters by rolling a broad leaf (D.H. Morse, unpubl. observ.). Other than *P. clarus*, only the sac spider *Clubiona bishopi* Edwards, 1958 (Clubionidae) oviposited in the shelters at this time. Several early juvenile *C. bishopi* occurred apart from their mothers, and had probably been recently abandoned in the shelters. Only in this species did more than one individual occupy a shelter. Small salticids made up the only other common group of spiders. Most or all of these consisted of mid to late instar *Pelegrina insignis* (Banks, 1892), an abundant salticid in the study area that made up 88% of the small salticid species there (Morse 2006); thus, a large percentage of young that were only tentatively identified probably belonged to this species. I found no sign of them nesting in these sites. They usually complete reproduction in the study area well before late summer (D.H. Morse, pers. observ.).

The dead and dried condition of the shelters probably minimized the potential for food gathering by the spiders, as few or no resources remained for herbivores, although first and second-instar fern moth caterpillars remained in some shelters. The dead and dry condition of the shelters probably also made them more difficult to manipulate, which might have minimized their occupancy. Earlier in the season, I have observed both *Xysticus emertoni* Keyserling, 1880 and *Phidippus clarus* removing *H. theseusalis* larvae from loosely constructed live shelters. I have also observed paper wasps *Polistes* sp. and bald-faced hornets *Dolicovespula maculata* attempting to force their way into shelters early in the season, as have Weiss et al. (2004).

The spiders preferred shelters on sensitive fern to those of marsh fern ($G_1 = 16.81$, $P < 0.001$, G test for independence), the major difference occurring in the distribution of *P. clarus* ($G_1 = 14.40$, $P < 0.001$, same test), although the combined remaining species also selected sensitive fern over marsh fern ($G_1 = 4.60$, $P < 0.05$, same test). The shelters on sensitive fern are more robust than those of marsh fern, and more likely to contain openings in these hardened structures that visitors can access (Fig. 1).

The number of spider species differed strikingly from those of a study reported from living fern shelters by Jennings et al. (2017) in eastern Maine, in spite of a roughly comparable number of individuals in the two studies. Jennings et al. (2017) identified 36 species vs. the eight species of spiders in my study (Table 3). Twenty-four of their species (66.7%) consisted of a single individual, vs. three of mine (37.5%). Miliczky et al. (2014) analyzed secondary occupants of live western alder leaf rolls made by lepidopterous larvae in Washington State. They recorded 17 species of spiders, five represented by a single individual (29.4%), as well as a wide range of insects. Thus, though the three studies all sampled large numbers of shelters (Table 3), they exhibited strikingly different numbers of species ($G_2 = 42.18$, $P < 0.001$ in G-test for goodness of fit) (post-hoc comparisons of each pair of species also significant). Branco et al. (2008) did not indicate the number of species in the nine spider families secondarily occupying shelters made by the larvae of the pine processionary moths *Thaometopoea piticampa* in Portugal, but noted that they accounted for approximately half of the arthropod diversity, thereby suggesting a species count comparable to the Miliczky et al. (2014) and Jennings et al. (2017) counts, rather than that of the present study.

Spiders made up over two-thirds of the arthropods in my study (excluding the early-instar fern moth caterpillars, as

Figure 1.—Shelters of fern moths *Herpetogramma theseusalis* (Crambidae) on ferns in July. Left: shelter on sensitive fern *Osmunda sensibilis*; Right: shelter on marsh fern *Thelypteris palustris*. Note the more open construction of the shelters on sensitive fern.

noted above). In contrast, Branco et al. (2008) and Miliczky et al. (2014) recorded a diverse group of insects, such that spiders represented only a minority of the arthropod fauna (Table 3) ($G_2 = 41.42$, $P < 0.001$, arcsin transformation). Jennings et al. (2017) did not comment in detail on other secondary inhabitants of their shelters.

The fern moth shelters did not appear to provide opportunities that favored additions to the modest species pool. All of the species I recorded commonly occurred in the fern habitat or in adjacent habitats, and the low numbers could also result in part from the low plant diversity of this habitat: two species of ferns (Morse 2011). The low diversity of spiders in the present study appears unlikely to result from an inadequate sampling routine, as my procedures resembled those of Jennings et al. (2017), and I regularly found cryptic species of other taxa in these shelters as well (mostly Hymenoptera and Coleoptera), further suggesting an adequately rigorous collecting regime.

Although jumping spiders numerically dominated my samples, sac spiders dominated all three of the other studies (Table 3). The percentage of salticids in the present study significantly exceeded that of the other studies ($G_3 = 65.60$, $P < 0.001$, arcsin transformation), while clubionids dominated that of the other three studies ($G_3 = 29.24$, $P < 0.001$, arcsin transformation). None of these authors recorded large jumping spiders, such as *P. clarus*, the main contributor to the present study.

Significantly different proportions of spiders occupied shelters in the four studies ($G_3 = 17.74$, $P < 0.01$, arcsin transformation). Only a small percentage of the shelters in my study area contained spiders, with markedly higher proportions in both the Jennings et al. and Miliczky et al. studies, although Branco et al. reported a result similar to my study (Table 3), perhaps a consequence of both studying dead shelters.

In a minor peculiarity, the presence of a single *Pardosa moesta* Banks, 1892 (Lycosidae) appeared most unusual: none of the other three studies recorded a wolf spider in their species lists. *Pardosa moesta* occur abundantly in the study area (D.H. Morse, pers. observ.), but in common with many other wolf spiders, it is a ground dweller rather than a shelter seeker. This record could represent a chance capture of an individual in an unusually low-lying shelter, but, unfortunately, my records provide no further information on it. The other species represented by one or two individuals in the present study (Table 2) all regularly construct shelters for oviposition or protection (e.g., Morse 2007; Bradley 2013).

In sum, the present study differed strikingly from the others; for the most part in being salticid-dominated rather than clubionid-dominated, with a low proportion of shelters

Table 3.—Comparison of frequency and composition of spider inhabitants in shelters made by lepidopteran larvae across four studies.

Study	Number of species.	Number of shelters	% of arthropods	% shelters with spiders	% of salticids	% of clubionids
This paper	8	3156	67.4	12.7	85.1	8.7
Branco et al.	-	2798	9.7	9.7	22.0	42.6
Miliczky et al.	17	5172	25.7	29.4	16.5	39.2
Jennings et al.	36	1074	-	35.1	14.3	42.6

containing spiders, and a low number of species. Spiders in the present study used shelters largely as nest sites, resulting primarily from the activity of a single species. The most similar study, that of Jennings et al. (2017) on ferns, censused live shelters suggesting that the condition of shelters (live or dead) may play an important role in the occupancy of spiders, as well as herbivorous prey.

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