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Jumping spiders (Salticidae) enhance the seed production of a plant with extrafloral nectaries

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Abstract Many plants secrete nectar from extrafloral nectaries (EFNs), specialized structures that usually attract ants which can act as plant defenders. We examined the nectar-mediated interactions between *Chamaecrista nictitans* (Caesalpineaceae) and jumping spiders (Araneae, Salticidae) for 2 years in old fields in New Jersey, USA. Previous research suggests that spiders are entirely carnivorous, yet jumping spiders (*Eris* sp. and *Metaphidippus* sp.) on *C. nictitans* collected nectar in addition to feeding on herbivores, ants, bees, and other spiders. In a controlled-environment experiment, when given a choice between *C. nictitans* with or without active EFNs, foraging spiders spent 86% of their time on plants with nectar. *C. nictitans* with resident jumping spiders did set significantly more seed than plants with no spiders, indicating a beneficial effect from these predators. However, the presence of jumping spiders did not decrease numbers of *Sennius cruentatus* (Bruchidae), a specialist seed predator of *C. nictitans*. Jumping spiders may provide additional, unexpected defense to plants possessing EFNs. Plants with EFNs may therefore have beneficial interactions with other arthropod predators in addition to nectar-collecting ants.

Key words Extrafloral nectaries · *Chamaecrista nictitans* · Jumping spiders · *Eris* sp. · *Metaphidippus* sp.

Introduction

Extrafloral nectaries (EFNs) are specialized plant structures that secrete nectar but are not associated with pollination. This nectar is collected by many arthropods, but the most frequently cited visitors to EFNs are ants that may protect the plant from herbivores and seed predators (Keeler 1980; Beattie 1985; Barton 1986). In many communities this has resulted in a general yet very effective plant defense mechanism (Koptur 1984). Recent papers have discussed other EFN visitors including parasitoids (Ruhren 1998) and predators such as Coccinelidae (Pemberton and Vandenburg 1993), mites (Pemberton 1993), and spiders (Taylor and Foster 1996).

To test the effect of jumping spiders (Salticidae) on plants with EFNs, we observed *Chamaecrista nictitans* (Caesalpineaceae), a native annual legume bearing EFNs. Little has been reported about the visitors and possible benefits of EFNs for *C. nictitans* and there have been no prior reports of spiders interacting with *C. nictitans*. Boecklen (1984) determined that ants visiting EFNs did not enhance the survival of the congener *C. fasciculata*. Although Barton (1986) listed more than 50 species of arthropods on *C. fasciculata*, spiders were not recorded. Many arthropod species also visit *C. nictitans*, but Ruhren (1998) determined that ants did not enhance the fitness of *C. nictitans*. However, our preliminary observations revealed that jumping spiders also collect nectar from *C. nictitans*.

The major objectives of these experiments were: (1) to determine the effect of *C. nictitans* patch size on the activity of jumping spiders; (2) to evaluate changes in fitness (mean fruit and seed number) facilitated by spiders; (3) to determine the effect of habitat on plant-insect interactions on *C. nictitans*, and (4) to determine if the novel guild of predators – jumping spiders – chooses plants with EFNs.

Ultimately, our study tested three main hypotheses: (1) the presence of EFNs and variation in patch size of *C. nictitans* will influence plant reproductive output; (2) individual plant fitness will vary with spider activity, and (3) EFNs will influence plant choice by spiders.

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Materials and methods

Study organisms

C. nictitans (Caesalpineaceae) is a low-growing annual legume with petiolar EFNs visited by many arthropods. Each *C. nictitans* plant may bear up to 30 inflorescences (one to five flowers per inflorescence) with 1–12 seeds produced per fruit (Ruhren 1998). *C. nictitans* grows in diverse habitats of the eastern United States including disturbed areas, open woods, and fields, all with well-drained soil (Lee 1989; Ruhren 1998). Each petiole has one EFN in close proximity to flowers and fruit and plants begin to produce nectar as the first leaf expands (Ruhren 1998). Jumping spiders (Araneae, Salticidae) were allowed free movement in and out of all field patches of *C. nictitans*. The 24 spiders used in the controlled environment experiment were captured at the field site.

Field investigation

Field work was initiated at Hutcheson Memorial Forest (HMF) in East Millstone (Somerset County), New Jersey, USA, in three fields dominated by perennial herbs. To test the role of plant patch size in promoting ant and associated arthropod activity and enhancing fitness, we planted *C. nictitans* seedlings in three old fields at HMF in May 1996 and 1997. Comparisons were made within and among these three fields. One plot was placed in each field and each plot was divided into an array of patches, 3 m apart.

Using an artificial array of plants, we manipulated plant densities in these field plots, leaving the surrounding vegetation undamaged. Experimental patch sizes exceeded those seen naturally. In 1996, patches of 2, 10 and 30 plants were planted. Patches of 2 and 30 plants were planted in 1997. Thirty patches were planted per field in 1996 and 40 patches in 1997. Patches were arranged with plants sufficiently close to create a single interconnected network of stems. Each year, the stems of a subset of patches were coated with Tanglefoot, a sticky compound that excludes arthropods, allowing comparison of plants with or without ants. These barriers were proven to be effective and did not damage the study plants (Boecklen 1984). Because *C. nictitans* has a single stem and an upright stature, coating an isolated stem at the soil surface effectively excluded non-flying insects. If surrounding vegetation created a bridge during the field season, it was moved. We enclosed each plot with a 2-m-tall deer exclusion fence, and surrounded each patch with a 30-cm-tall barrier of hardware cloth to reduce small-mammal damage.

All plants were monitored for insect and spider activities and interactions between 0800 and 1700 hours for approximately 3 days per week from late May until the end of August. Ant and spider identity and behavior were recorded for each plant along with the time they spent foraging and interacting with other arthropods. Data included organism counts and the timing, duration, and outcome of interactions. All fruit were collected as they matured just before dehiscence and were analyzed by treatment.

Greenhouse experiment

Starting on 22 August 1997, we observed jumping spiders in 38-l terraria in the greenhouse. In each of six terraria, two pots – each containing three mature *C. nictitans* – were placed at either end for a total of four pots and 12 plants per terrarium. Within each enclosure, one pair of potted plants was chosen at random to have the EFNs covered with a drop of clear nail polish. This was repeated for all terraria, rendering 50% of *C. nictitans* functionally nectar free. After the polish had dried, a single spider was released into each terrarium. These were closed with screen lids to prevent spider escape, but allowing free movement of microarthropods, potential prey for the spiders. Spiders had free access to both water and prey.

To determine plant choice and spider behavior, we observed each terrarium for approximately 6 h (30-min intervals) per day for 4 days. At the end of the 4 days, resident spiders were removed, polish was restored on the EFNs, and new spiders were placed with the plants (total of 24 spiders in the experiment). The procedure was replicated four times and the same plants were used for all replicates.

Data analysis

For field experiments, fruit and seed set were analyzed with a mixed-model ANOVA with field as a fixed effect, and patch size, ant exclusion, and presence or absence of spiders as random sources of variation. Post hoc comparisons of means were run within years and among patches and fields. Mean fruit and seed production per treatment were compared. The numbers of spiders were analyzed among patch sizes, fields, and ant treatment. Data from 1996 and 1997 were analyzed separately because of altered experimental design and different weather conditions.

Data from the greenhouse spider observations were summarized separately. Percentage of time on *C. nictitans* and time spent on plants with active EFNs were compared.

Results

Fruit and seed set were significantly higher for plants with spiders present in 1996 ($df = 1$, $P = 0.0001$; Fig. 1). In 1997, fruit set was not significantly different for plants with spiders, but seed set increased by 8% in plants with spiders ($df = 1$, $F = 3.988$, $P = 0.04$).

Predation by spiders [*Eris* (syn. *Paraphidippus*) sp. and *Metaphidippus* sp.] was recorded infrequently but we did witness spiders eating ants (*Crematogaster* sp.), herbivores, and several bees (*Dialictus* sp., Halictidae). Many

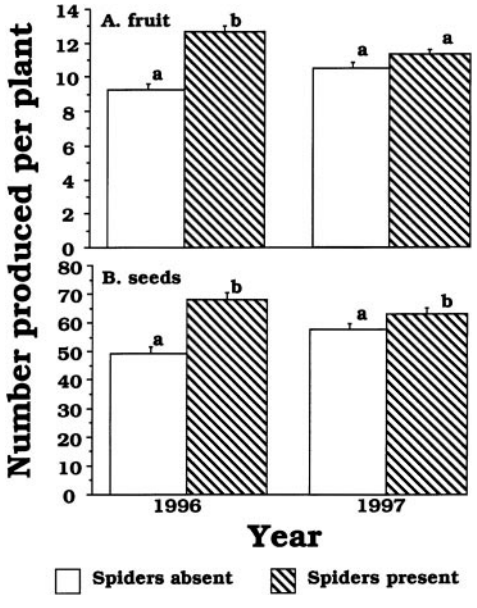

Fig. 1 Mean production (plus SE) of fruit and seeds by *Chamaecrista nictitans* as a function of jumping spider presence in field patches of varying sizes in 1996 and 1997. Years were analyzed separately. Bars marked with different letters are significantly different (SNK, post hoc means comparison, $P < 0.05$)

other visitors were directly attracted to EFNs on *C. nictitans* in both years (Ruhren 1998). Ants, parasitoid wasps, bees (Halictidae), and spiders collected nectar, but herbivores did not collect nectar in either year.

A specialist seed predator (*Sennius cruentatus*, Bruchidae), was detected in *C. nictitans* pods in 1997. Spiders had no significant effect on *S. cruentatus* in *C. nictitans* ($df = 1$, $F = 1.75$, $P = 0.20$). Of those plants with *S. cruentatus*, 46% were visited by spiders. More plants in large patches had bruchids in their pods; however, the mean number of beetles per attacked small patch was significantly greater [small patch mean = 3 (1.1 SE); large patch mean = 1.5 (0.18 SE); ANOVA $df = 1$, $F = 5.01$, $P = 0.034$].

Plant patch size had a significant effect on the number of visitors per patch in both 1996 and 1997. Field did not have a significant effect on the number of ants, spiders, or herbivores per *C. nictitans* patch (Ruhren 1998). The number of spiders per patch per year increased with patch size. Patch sizes and mean number of spiders (± 1 SD) were as follows: 1996 – 2 plants, 0.14 ± 0.35 spiders; 10 plants, 0.86 ± 1.41 spiders; 30 plants, 1.17 ± 1.15 spiders; 1997 – 2 plants, 0.25 ± 0.68 spiders; 30 plants, 2.24 ± 2.45 spiders. The number of spiders differed significantly with patch size (1996: $df = 2$, $F = 11.500$, $P = 0.0001$; 1997: $df = 1$, $F = 36.679$, $P = 0.0001$). However, the number of spiders per plant was not significantly affected by patch size (1996: $df = 2$, $F = 0.979$, $P = 0.379$; 1997: $df = 1$, $F = 1.308$, $P = 0.255$). Spider numbers were not significantly related to the presence or absence of ants on *C. nictitans* (ANOVA, $P > 0.01$).

In the greenhouse experiment, spiders spent 42% of the time on *C. nictitans* ($df = 1$, $\chi^2 = 1.3$, $P > 0.05$), and chose plants with active EFNs six times more frequently than *C. nictitans* with inactivated EFNs ($df = 1$, $\chi^2 = 47.5$, $P < 0.01$). Spiders did feed at the EFNs, collecting nectar with their chelicerae.

Discussion

The presence of jumping spiders was correlated with increased seed set by *C. nictitans*. The mechanism of this benefit was not directly observed but may be attributed to direct consumption or deterrence of herbivores and seed predators. Louda (1982) reported that more flowerheads survived on *Haplopappus* plants with spiders. According to Louda (1982), these sit-and-wait predators thrive on flower patches with a steady supply of herbivores and pollinators.

Salticid spiders, often the dominant taxa of non-webbuilding spiders within terrestrial communities (Breene et al. 1993), are commonly described as carnivores, only consuming moving prey (Foelix 1982; Riechert and Harp 1987). However, several authors have reported incidences of nectar-feeding (Pollard et al. 1995; Taylor and Foster 1996) and less restricted spider diets (Smith and Mommsen 1983). EFNs supply both carbohydrates and water (Pollard et al. 1995) and frequently amino acids and lipids (Keeler 1980; Pemberton 1993). Nectar may help sustain spiders and prevent dehydration (Pollard et al. 1995; Taylor and Foster 1996). However, nectar consumption may be overlooked because of the nocturnal habits of many spiders (Taylor and Foster 1996).

Furthermore, spiders may be attracted to prey feeding at EFNs. Spiders often locate higher prey areas (Riechert 1974); larger patches of *C. nictitans* attracted more visitors, including herbivores and spiders. Spider numbers are often stable within a community, allowing these predators to respond quickly to prey increases (Riechert 1974), frequently migrating to patches with more abundant prey (Riechert 1974). Larger patches of *C. nictitans* which also attracted more plant hoppers, potential spider prey (Döbel et al. 1990), attracted and maintained more jumping spiders. Crab spiders often select high-quality inflorescences, containing the most prey and nectar (Morse 1986). Riechert and Harp's (1987) results support our observations, suggesting that solitary spiders maintained residency on individual patches of *C. nictitans* for several days. Therefore, plants may influence both prey numbers and behavior and hunting success of spiders (Hatley and MacMahon 1980). Because choice of an area is often correlated with access to prey by spiders (Morse 1986; Riechert and Harp 1987), EFNs, such as like those on *C. nictitans*, may increase hunting success while reducing the hunger and wandering of these predators. The role of EFNs in maintaining a local spider population should be tested on other plants.

Although the presence of jumping spiders on *C. nictitans* appears to benefit this plant, certain plant visitors may be able to avoid or are protected from predation by jumping spiders (Foelix 1982). *S. cruentatus*, the specialist seed predator discovered in fruit of *C. nictitans*, is most likely well defended from jumping spider attacks because of physical and phenological traits; the sclerotinized beetles develop within the maturing fruit, shielded from both spiders and ants. However, we were unable to test this because we did not observe direct interactions between ovipositing female beetles and patrolling spiders.

Reports of spiders and other non-ant EFN visitors (Knox et al. 1986; Pemberton 1993) highlight the possibility for broad beneficial interactions based on EFN use, some of which may be even more beneficial than the ant-plant relationship. In addition to the mutualisms with ants in many habitats (Koptur 1984), EFNs could facilitate a general, very effective plant defense mechanism. This may be more effective than if the plants were associated with solely the ant guild of the arthropod community.

Ecological relationships between most EFN plants and their visitors are facultative (Koptur 1992). A diversity of organisms visit EFNs, and a variety of positive direct and indirect outcomes for the plant may be facilitated by EFNs. The non-specific effect of many

suitable plant visitors could benefit plants having EFNs when colonizing new habitats (Bentley 1976). In fact, it is the general, cumulative response to EFN nectar that is being supported and not necessarily a narrow coevolved mutualism. Variation in arthropod communities, coupled with the frequent expansion or initiation of plant populations, should support the selection of a general reward such as extrafloral nectar (Beattie 1985). Frequently overlooked predators, such as jumping spiders – attracted and supported by EFNs – may be contributing significantly to plant defense in many communities.

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