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Crab spiders deter insect visitations to slickspot peppergrass flowers

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Insects visiting the flowers of slickspot peppergrass, *Lepidium papilliferum* (Brassicaceae), risk predation by crab spiders, *Misumena vatia* (Thomisidae). In a field study conducted at two sites in southwestern Idaho, 7.5±2.7% of *L. papilliferum* plants (range 0–30%, N = 16 surveys of up to 40 randomly selected plants) harbored a crab spider. However, through 205 minutes of observations at plants with a spider, only 15 predation attempts were observed, with only 3 of those being successful. Despite the relatively low incidence of predation by crab spiders, an experiment revealed that the number of insects visiting *L. papilliferum* flowers was significantly lower at plants that harbored a crab spider than at plants free of spiders. In another experiment, floral visits increased significantly following the removal of crab spiders from individual plants. The deterrent effect of spiders was not due to a disproportionate avoidance response by certain types of insects; all insect families included in our analysis showed decreases in visitations to flowers when spiders were present, although none of these differences were statistically significant at the individual level. We found no significant change in the duration of visits to plants harboring a spider, implying either that the visitors were oblivious to the predator's presence, or that they were aware of the predator but kept their distance. Our study is one of a growing number to find a decrease in floral visits in response to predators, suggesting that the phenomenon is more widespread than was previously recognized.

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Insects that consume pollen and nectar risk capture by other arthropods that use flowers as hunting sites. Although predation risk has long been considered an significant selective force in the evolution of behavioral traits in animals (Lima and Dill 1990, Peacor and Werner 2000), the importance of predation risk on the activity and behavior of pollinators has typically been viewed as negligible (Morse 1986, Wilkinson et al. 1990, Schmalhofer 2001). The rationale for this assertion is that predation rates have generally been low (e.g. <2% in Morse 1986, <3% in Schmalhofer 2001), and foragers have shown no signs of avoiding predators (Morse 1986, Wilkinson et al. 1990).

The observed lack of a response to predators under natural conditions is at odds with several laboratory studies that have shown that bees exhibit sensitivity to predation risk (Cartar 1991, Craig 1994, Dukas 2001), including the selection of safe flowers over equally rewarding yet potentially dangerous alternatives (Dukas 2001). Moreover, a growing number of field studies have found a decrease in floral visits in response to predators (Dukas and Morse 2003, Suttle 2003, Muñoz and Arroyo 2004), suggesting that the phenomenon may be more widespread than previously recognized. Here we report on a field study that examined whether floral visitors to slickspot peppergrass, *Lepidium papilliferum* L. (Brassicaceae), avoid plants harboring the crab spider, *Misumena vatia* Clerck (Thomisidae).

M. vatia has been described as an opportunistic, rather than selective, hunter based on the observation that it attacks virtually all insects within striking distance (Morse 1979). However, not all potential prey are

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equally vulnerable to capture by crab spiders. Morse (1979) found that while 39% of attacks on small syrphid flies were successful, the success rate dropped to 1.6% for attacks on bumble bees. Similarly, Morse (1986) reported that *Apis mellifera* and *Bombus ternarius*, both relatively small bee species, were more vulnerable to capture by *M. vatia* than were two larger *Bombus* species. Dukas and Morse (2003) suggested that these differences in vulnerability to capture may explain why the two smaller bee species in their study exhibited greater avoidance of milkweed patches containing *M. vatia* than did the larger species. Thus, vulnerability to predation may influence predator avoidance behavior. Because the insects that visit *L. papilliferum* vary widely in size (from 2 to 25 mm in body length) and defensive ability (stinging hymenoptera vs non-stinging insects; soft-bodied insects vs hard-bodied insects), we were interested in determining whether avoidance behavior would reflect species-specific differences in vulnerability as prey.

Slickspot peppergrass is a rare mustard endemic to sagebrush-steppe habitat in southwestern Idaho. Within sagebrush areas, the plant is limited to microsites known as "slick spots", which are characterized by their high levels of clay and salt as well as by soil water retention that is higher than that of surrounding areas (Quinney 1998). Flowering generally extends from early May to late June. The plant reaches 10 to 40 cm in height and has numerous, multi-flowered inflorescences that terminate at the branches. A wide variety of insects attend the plant's small white flowers, and these insects are essential for pollination and fruit production (Robertson and Klemash 2003). Juvenile crab spiders are sometimes found on, or tucked among, *L. papilliferum* flowers, where they remain relatively motionless with their forelegs outstretched in wait of insects that venture too close.

In this study we recorded the frequency of occurrence of crab spiders on *L. papilliferum*, and we documented incidences of attempted and successful prey capture. To evaluate whether insects foraging on the flowers avoided plants harboring a predator, we compared the number of visitations by insects on plants with a crab spider to those without. We also conducted a manipulative experiment, with appropriate controls, in which visitations by foraging insects were recorded while a crab spider was present on a plant, and again shortly after the spider had been removed.

Methods

We conducted our study in June 2003 at two *L. papilliferum* populations (PL and ART) located 6.5 km apart within the Orchard Training Area of the Idaho Army National Guard in southwestern Idaho (43°20′N, 116°10′W). Both sites contained more than 500 individual *L. papilliferum*. At each site we regularly surveyed *L. papilliferum* for the presence of *M. vatia*. During each survey we walked throughout the site and randomly selected a total of 40 plants; in two instances we surveyed only 26 and 34 plants. Plants were selected at a distance of several meters from the observer, which was too far to determine the presence or absence of spiders. We then moved close to the selected plant and searched for a spider. When we found a spider, we noted whether it held prey in its chelicerae, and if it did, we recorded the identity of the prey. We did not revisit plants during a particular survey, although it is possible that some plants were revisited during subsequent surveys on different days during the study. Because *M. vatia* typically do not remain on individual plants for more than a few hours (pers. obs.), we feel justified in treating each survey as an independent sample. To augment our data on the diet breadth of *M. vatia*, we opportunistically noted the identity of any prey items in the chelicerae of spiders we encountered while conducting other aspects of our research. Some of these observations were made in June, 2004 and added to our data from 2003.

Throughout the study we conducted a series of observations to determine whether insect visitations to flowers were less frequent on *L. papilliferum* plants when spiders were present than when they were absent. We began by searching for a plant with a spider because these plants were less commonly encountered than plants without spiders. When we located a suitable plant, we measured its height and then monitored the plant for five min from a distance of about 1 m. We noted the identity (to family) of all insects that landed on at least one of the plant's flowers, and we recorded the total duration of each insect's visitation using a stopwatch. A visitation was defined as the period during which an insect foraged continuously at the plant's flowers. If the insect left the vicinity of the plant and then returned, we counted two visitations. During visitations we noted any attempted or successful prey captures by crab spiders. If an insect's foraging was interrupted by a spider attack or interaction with another insect, the duration of the visit was excluded from analysis. Once the observation period was complete, we selected a nearby plant (<2 m away) of similar size and condition, but without a spider, and then began another five-minute observation period. Because the frequency of insect visitations to plants may have changed over the consecutive observation periods, independent of a spider's presence (e.g. due to acclimation to the observers, or shifts in insect abundance), we conducted a control in which two similarly-sized plants without spiders were monitored consecutively for five min.

Alternating with pairs of trials in the observational study, we conducted an experiment to determine whether the removal of a spider from a plant resulted in an increase in the number of insect visitations to the plant. We were unable to conduct the counter-experiment, i.e. the addition of a spider to a plant, because spiders added to plants fled immediately. Following the protocol described above, we located a plant with a spider, and then monitored it for insect visitors for five min. Following this observation period, we carefully removed the spider from the plant by corralling it into a vial, waited five min, and then began a second five-minute observation period. We returned the spider to the plant following the experiment. Because our observations and handling of the plant may have influenced insect visitations, we conducted a control in which we monitored a plant without a spider for five min, jostled the plant to simulate the removal of a spider, and then monitored it again for five min following a five-minute waiting period.

We tested our data for normality using a Kolmogorov–Smirnov (Lilliefors) test, and for homogeneity of variance using Levene's test (Wilkinson et al. 1992). When data did not meet the requirements for parametric analysis we used a non-parametric equivalent. When we conducted multiple tests on a data set, we used sequential Bonferonni correction (Rice 1989) to adjust alpha levels. All reported p-values are two-tailed.

Results

We found *M. vatia* on 8 of the 394 plants surveyed at ART (2.0%, based on a total of 10 surveys), and 36 of 226 plants surveyed at PL (15.9%, based on a total of 6 surveys). The occurrence of spiders at ART was more-or-less constant throughout the sampling period, whereas at PL it was as high as 30% during the first half of the study and then dropped to about 2% during the second half of the study. Nine of the spiders found during the survey held prey in their chelicerae. An additional 17 prey captured by crab spiders were recorded via opportunistic encounters throughout the study period. Table 1 summarizes the identity and number of prey found. Note that no inference about prey preferences is implied by the distribution of prey types.

Table 1. Identity and quantity of prey found captured by crab spiders.

Order	Family	Number
Hymenoptera	Apidae[†]	2
	Halictidae	8
	Sphecidae	5
	Vespidae	1
Diptera	Asilidae	2
	Bombyliidae	2
	Syrphidae	2
	Tachinidae	2
	unidentified	1
Lepidoptera	Gelechiidae	1

[†] *Apis mellifera* (Apidae) were observed in 2004 at a different site from where experiments were conducted in 2003.

Insect visitations were significantly higher on plants without a spider than those with a spider (Fig. 1a; paired t-test, t = 3.21, df = 20, P = 0.004). Although larger plants attract more insects than smaller plants (Robertson and Klemash 2003), the plants in our paired comparisons did not differ significantly in size (paired t-test, t = 0.47, df = 20, P = 0.66). Also, we found no significant increase in visitations between the first and second observation periods in our controls (Fig. 1b; paired t-test, t = 0.46, df = 19, P = 0.65), reducing the likelihood that differences in insect abundance in our experiment were caused by acclimation of insects to the observer. Although we found a significant overall trend for plants without a spider to have higher insect visitations than those with a spider, we found no statistically significant differences when insect families were considered separately. However, in all cases the mean number of visits was higher when spiders were absent (Table 2a). The presence or absence of a spider had no significant influence on the duration of visits by individual insect families (Mann–Whitney U-tests; all P > 0.1).

Consistent with the results of our observational study, insect visitations to plants increased significantly following the removal of a spider (Fig. 2a; paired t-test, t = 2.49, df = 21, P = 0.02). In the control trials, we found no significant difference in insect visitations between the first and second observation periods (Fig. 2b; paired t-test, t = 0.56, df = 19, P = 0.58). This similarity suggests that removal of the spider caused the increase in insect visitations in our experiment. Although we found no significant differences in visitation for individual insect families following spider removal, for all five families the mean number of visitations increased (Table 2b).

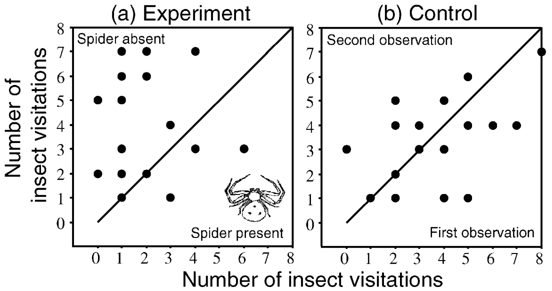

Fig. 1. (a) Results of the observational experiment. Each data point represents the number of insect visitations to a plant with a spider (x axis value) relative to the number of insect visitations to its paired counterpart without a spider (y axis value). Points falling above the 1:1 line indicate that more insects visited the plant without a spider than the plant with a spider. (b) Results of the control. Each data point represents the number of insect visitations to a plant during the first observation period (x axis value) relative to the number of insect visitations to its paired counterpart during the subsequent observation period (y axis value). Note that the points fall more-or-less evenly above and below the line.

Table 2. Mean visitation rates of individual insect families in the (a) observational study (N = 21 pairs of observations) and (b) spider removal experiment (N = 22 pairs of observations). Only families encountered in five or more observation periods are included individually in the table. Remaining families are grouped as "Others".

a) Observational study

Order	Family	Mean (±SE) number of visits		
		Spider present	Spider absent	P value†
Hymenoptera	Halictidae	0.43±0.16	1.09±0.34	0.12
	Sphecidae	0.24±0.14	0.29±0.14	0.72
	Vespidae	0.19±0.14	0.47±0.19	0.23
Lepidoptera	Gelechiidae	0.14±0.10	0.33±0.20	0.26
Coleoptera	Melyridae	0.38±0.11	0.95±0.28	0.049*
Others		0.28±0.12	0.81±0.27	0.045*

b) Spider removal experiment

Order	Family	Mean (±SE) number of visits		
		Spider present	Spider removed	P value†
Hymenoptera	Halictidae	1.10±0.30	1.40±0.30	0.36
	Sphecidae	0.18±0.11	0.59±0.20	0.06
	Vespidae	0.13±0.10	0.18±0.08	0.58
Coleoptera	Melyridae	0.77±0.28	1.13±0.32	0.10
Diptera	Bombyliidae	0.36±0.20	0.54±0.28	0.48
Others		0.59±0.23	0.36±0.22	0.06

†paired t-test.
*not statistically significant following sequential Bonferonni correction.

The removal of the spider did not influence the duration of visits by individual insect families significantly (Mann–Whitney U-tests; all P > 0.2).

We witnessed three successful predation events during the five-minute observations on plants with spiders; two halictid bees and one robber fly (Asilidae) were captured. We also observed 12 failed predation attempts; six halictid bees, one gelechiid moth, one vespid wasp, and four melyrid beetles. In the case of the failed attempts on melyrids, spiders successfully captured the beetles and then released them without a struggle. At other times during our study we observed a failed attempt on a tachinid fly, two failed attempts on gelechiid moths, plus a successful capture a gelechiid moth, followed by its immediate release. Almost all insects that escaped predation immediately left the vicinity of the plant and generally the slick spot. To our knowledge, these insects did not return to the plant during the observation period. In one case, a halictid bee escaped a predation attempt only to return to the same spot on the plant for a second capture by the spider. The bee escaped again, and finally left the area.

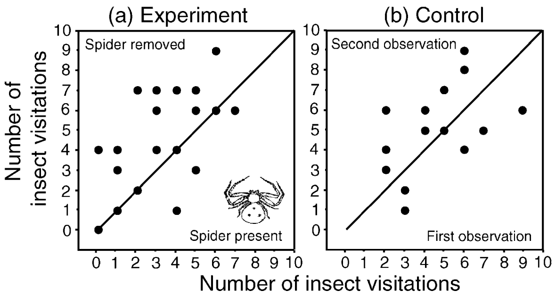

Fig. 2. (a) Results of the spider removal experiment. Each data point represents the number of insect visitations to a plant with a spider (x axis value) relative the number of insect visitations to the same plant following the spider's removal (y axis value). Points falling above the 1:1 line indicate that more insects visited the plant following the spider's removal. (b) Results of the control. See Fig. 1b legend for explanation.

Discussion

The presence of crab spiders on individual *L. papilliferum* plants significantly reduced the number of insect visitations to those plants, in both our observational study and manipulative experiment. This reduction in visitation may be explained either by direct or indirect effects of predation (Dukas and Morse 2003). A direct effect would mean that crab spider predation at a plant reduced the number of insects available to visit that plant. However, this explanation is not plausible in our study because it would require that individual insects confined their foraging to individual plants, which is not the case on *L. papilliferum*. Having studied insect-mediated pollination of *L. papilliferum* for several years, we have observed that flower-visiting insects regularly move between plants, as well as between slick spots, while foraging. An additional weakness of the direct effects hypothesis is that it cannot account for the increase in insect visitations recorded following the removal of spiders from plants.

Indirect effects of predation would mean that insects avoided foraging at plants with a predator (reviewed for flower-visiting insects by Dukas 2001). Despite the cryptic appearance and behavior of *M. vatia*, insects could have gained knowledge of a spider's presence in several ways and therefore avoided the plant while foraging. A spider's unsuccessful attack on an insect is the most obvious indication of the predator's presence. In our study, unsuccessful attacks almost always resulted in the insect leaving the vicinity of the attack, and typically moving out of the slick spot entirely. Although we cannot be certain, it seems likely that these insects did not return to forage at the plant, at least in the short term. Thus, their departure, either before or during our five-minute observations on plants with spiders, may account for some of the reduction in insect visitations we detected. Moreover, the commotion caused by an unsuccessful predation attempt may have alerted other insects to the presence of a spider, again resulting in a decrease in visitations, or at least greater vigilance by those alerted to the predator's presence. More subtle clues to a spider's presence may also have played a role, such as when a spider repositioned itself or when it attempted to stalk intended prey. We also cannot ignore the possibility that some insects may have detected spiders that were sitting motionless in wait of prey, although the limited attention capability of insects (Dukas 1998) makes this option less likely.

Only a few studies have reported predator avoidance by insects foraging on flowers in nature. Muñoz and Arroyo (2004) found that lizards reduced visitations by satyrid butterflies and syrphid flies to the flowers of *Chuquiraga oppositifolia* (Asteraceae), with a concomitant decline in seed output by the plant. Suttle (2003) found that crab spiders reduced the frequency and duration of floral visits by pollinating insects to ox-eye daisy, *Leucanthemum vulgare*. Finally, Dukas and Morse (2003) report that *Bombus ternarius* visited patches of milkweed less frequently when crab spiders were added to a patch than when the patches were free of spiders. Other studies on predator effects on flower visitation indicate that insects were unresponsive to predators (Morse 1986, Wilkinson et al. 1990). This lack of responsiveness, as well as low incidences of predation, has lead some to conclude that predation must not play a significant role in shaping the foraging behavior of flower visitors (Pyke 1979, Morse 1986, Schmid-Hempel 1991, Schmalhofer 2001). However, this interpretation may be flawed because lack of predation may actually be evidence for the evolution of successful predator avoidance strategies (Ydenberg 1998). Likewise, the inability of prey to detect predators does not necessarily indicate the absence of selection pressure to evolve such capability. If the selection pressure to evolve better predator-detection capabilities is countered by adaptations by the predator to escape detection, it may only appear that predation is of little evolutionary significance (Dukas 2001).

During the study we witnessed only 15 predation attempts during a total of 41 five-minute observations on plants harboring a crab spider. Only three of those attempts resulted in successful prey capture. That number translates into a prey capture for every 68 min that a spider forages. For an individual insect, the risk of predation while foraging at flowers is typically small, although it would vary depending on the local abundance of spiders. As an illustration, consider a site where 5% of the plants harbor a foraging crab spider. A randomly foraging insect would, on average, be captured by a spider after 1 360 minutes of foraging (22.7 hours) if it were the only insect visiting flowers. The risk to an individual insect would decline if multiple insects were present at the plant, due to the dilution effect. Not factored into the calculation is that insects differ in their vulnerability to capture following an attack (Morse 1979), and that spiders are unavailable as predators while they handle and consume prey, as well as when satiated from earlier meals. Nevertheless, despite the relatively low incidence of successful predation by crab spiders in our study, flower-visiting insects were deterred from visiting plants with spiders, suggesting that predation by crab spiders is, or has been, an important selective force on the foraging behavior of these insects.

Although we found a significant overall reduction in insect visitations to plants with crab spiders, this reduction was not due to a disproportionate avoidance response by certain types of insects. Rather, the trends in our data suggest that crab spiders deterred all flower-visiting insects from visiting plants (Table 2). Consistent with this result, we found no evidence that crab spiders were particularly choosy of their prey, apart from the five cases of spiders releasing the insect (four melyrid beetles and one gelechiid moth) they had captured. Because melyrids are small (ca 2 mm long) and hard-bodied, they may not be a very profitable meal relative to other prey types. In our study, insects from 3 orders and 10 families were represented in the diet of *M. vatia*. As others have found (Morse 1981, 1986, Wilkinson et al. 1990, Dukas and Morse 2003), *M. vatia* had no difficulty immobilizing hymenoptera, despite the large size of some (e.g. apids and sphecids) and their capacity to sting. Had some of the insects foraging on *L. papilliferum* been too large for *M. vatia* to effectively capture and consume, we predict that those insects would exhibit less in the way of avoidance behavior to crab spiders.

Flower-visiting insects are clearly at risk of predation when visiting *L. papilliferum* plants harboring crab spiders. That some insects foraged at these plants nevertheless suggests either that the insects were oblivious to the predator's presence, or that they were aware of the predator but kept their distance. The former explanation may help account for the observation that the presence of a spider did not influence visitation duration, even though there was an overall reduction in the number of visitations to the plant. Insects naïve about the presence of spiders may have foraged normally, whereas insects aware of the spider's presence may have completely avoided the plant. Additional research is needed to establish whether insects forage on plants known to harbor a spider, and if so, whether they modify their foraging behavior to reduce the risk of predation.

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