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Distribution of *Peucetia viridans* (Araneae: Oxyopidae) on Croton ciliatoglandulifer

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ABSTRACT Peucetia viridans (Hentz) lives almost exclusively on Croton ciliatoglandulifer (Ortega) in the dry forests of western Mexico. This spider is usually found on pubescent shrubs. Within their host plants, *P. viridans* has been associated with plant height and cover, as well as with number of flowers or inflorescences in anthesis. Flowers can be used as cues of good habitat conditions or because they attract prey detected by the spider. In this study, we assessed the importance of flowers, plant cover, and plant exposure (sun/shade) on the spider distribution in five 50-plant transects. In a field experiment, we also compared the number of spiders between controls, plants from which inflorescences were removed, and plants with artificial inflorescences. The results from the transects indicate that, when the number of flowers per spider is high, spiders were more abundant in exposed locations, which presumably offer better microclimatic conditions; when flowers become scarce, food may be more difficult to find and the spider distribution become strongly associated with the number of flowers, where they are more likely to find prey. Spider abundances on the experimental plot decreased on plants from which flowers were removed in comparison to control plants. Spider abundance increased on those in which artificial inflorescences were added. The similarity between plants with natural and artificial inflorescences suggests that spiders use flowers as cues of good microhabitats instead of prey visitors, which are significantly less abundant on artificial inflorescences.

KEY WORDS microhabitat use, inflorescences, sun exposure, Oxyopidae, tropical dry forest

Foliage-dwelling spiders have been associated with plant cover (Halaj et al. 1998), foliage density (Gunnarsson 1996, de Souza and Martins 2005), leaf surface area (Evans 1997), and number of leaves per branch (Halaj et al. 1998, de Souza and Martins 2005, Corcuera et al. 2008). Several studies have shown that these characteristics are related to habitat heterogeneity, refuge from predators, prey abundance, and suitable thermal conditions (Riechert and Tracy 1975; Gunnarsson 1990, 1996; Sundberg and Gunnarsson 1994; Halaj et al. 1998; Raizer and Amaral 2001). In addition, spiders of various guilds have been associated with the number and type of inflorescences of several plants (de Souza and Módena 2004, de Souza and Martins 2005, Morse 2007). Some crab spiders, for instance, use flowers that match their color and therefore can ensnare their prey without being detected (Heiling et al. 2003, Morse 2007). Other spiders are less selective, and their distribution is determined by trade-offs between prey availability and predators. The presence of inflorescences in the shrub Psychotria carthagenensis Jaquin (Rubiaceae), for example, had no significant effect on spider abundance because the inflorescences

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were densely occupied by ants, which may displace both the spiders and their potential prey (Faria and Lima 2008). In another study, de Souza and Módena (2004) found that hunting spiders (Oxyopidae and Salticidae) were equally common on three different types of inflorescences; however, larger individuals were more common on those that offered better refuge against predators.

Many lynx spiders (Oxyopidae) are found on plants with trichomes (Vasconcellos-Neto et al. 2007). Peucetia viridans (Hentz), in particular, has been found on Cnidoscolus aconitifolius (Mill.) I. M. Johnstone and Croton capitatus (Hogwort) (Euphorbiaceae), as well as Eriogonum fasciculatum (G. Bentham) (Polygonaceae), Gossypium spp. (Malvaceae), and Haplopappus venetus Blake (Asteraceae) (Brady 1964, Louda 1982, Randall 1982, Simpson 1995, Arango et al. 2000). Vasconcellos-Neto et al. (2007) suggested that *Peucetia* species select these types of plants because arthropods are trapped by the trichomes and represent available prey for the spider. Furthermore, recent evidence supports that a facultative mutualism between Peucetia, and its host plants is mediated by glandular trichomes (Romero et al. 2008), but not by reproductive structures (i.e., flowers, Morais-Filho

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and Romero 2008). Although the accumulated evidence indicate that this association is specific and predictable (Morais-Filho and Romero 2008), other factors also seem to be important in understanding which plant traits are involved in the specific association between *Peucetia* and its host plants. In this sense, presence of inflorescence and plant size could generate variation on the distribution of *Peucetia* individuals within their host plants. In particular, some studies suggest that P. viridans selects taller plants with a higher cover and panicles in anthesis (Louda 1982, Arango et al. 2000). Additionally, the green lynx spider, as well as other spiders, chooses plants under cover to avoid desiccation during extreme weather (i.e., the hot months in Southern Mexico and the dry cold season in Southern Brazil) (Arango et al. 2000, Romero and Vasconcellos-Neto 2004). As Riechert and Tracy (1975) pointed out, spiders might favor certain individual plants because of their ability to modify the thermal environment.

Previous studies in a tropical dry forest in Jalisco, Mexico, showed that P. viridans lives almost exclusively on Croton ciliatoglandulifer Ortega (Euphorbiaceae) (Corcuera et al. 2008) and that the occurrence of spiders is positively associated with plant cover and number of inflorescences but not with plant height (Jiménez-Salinas and Corcuera 2008). In the P. viridans-C. ciliatoglandulifer system, we also found no evidence of spiders preying on insects ensnared on the plant hairs (P.C., unpublished data). The main prey of P. viridans were wasps, bees, leafhoppers, and flies (80% of the insects trapped, n = 29 spider-prey encounters; P.C., unpublished data) that were found near the inflorescences but never entwined in the trichomes. To further understand the spider-plant relationship, we studied the importance of number of flowers in anthesis, foliage cover, and inflorescences of C. ciliatoglandulifer in the distribution of P. viridans. Because plant exposure has been linked to the distribution of Peucetia spiders (Arango et al. 2000, Romero and Vasconcellos-Neto 2004), we also evaluated if plant exposure (i.e., exposed/unexposed plants) influenced the spider distribution. These predictions were explored in five transects in a field survey. Finally, to assess the importance of inflorescences on spider abundance, we conducted a field experiment to test the following hypotheses: (1) plants with inflorescences represent high-quality patches in comparison to plants without inflorescences and (2) if flowers are used as cues of prey availability, spiders would be equally common on plants with natural inflorescences and plants from which natural flowers were replaced by artificial flower heads. We monitored changes in spider abundance on plants from which flowers were removed and compared them with those plants with natural and artificial inflorescences. If spiders use inflorescences as indicators of better microhabitat conditions or resource availability (i.e., pollinator insects), they would desert plants from which inflorescences were removed, whereas control plants would show high spider abundance. This aspect has not been assessed for the Peucetia-host plant system

before. This study will also elucidate whether the relative importance of some key factors used by the green lynx spider to select individual plants vary in time and with respect to resource availability.

Materials and Methods

Study Site and Species. The study was conducted in the state of Jalisco in western Mexico (between 20°20'42" and 20°22'16.4" N and 103°40'31" and 103°45′26″ W; altitude 1,380 m). Mean annual temperature was 20.3°C, and mean annual precipitation was 826 mm. The rainv season starts in June and ends in September. C. ciliatoglandulifer is a shrub with glandular stipules and monoecious inflorescences that flower from January to November (Martínez-Gordillo 1996). C. ciliatoglandulifer is a dominant shrub in the study area. The green lynx spider, P. viridans, is a cursorial hunting species that preys on a variety of insects and spiders, including individuals of its own species, up to 2.5 times larger than itself (Turner 1979; Nyffeler et al. 1987, 1992). It is common on wild flowers, grasses, and low shrubs (Whitcomb and Easton 1967, Nyffeler et al. 1992). It is an annual univoltine that breeds and lays its eggs in summer and autumn. Dispersal by ballooning occurs during the winter (Corev and Taylor 1989). The study was conducted from September to December 2007, which includes the peak of the breeding season of *P. viridans*, and follows a preliminary surveillance carried out in autumn 2004 (Jiménez-Salinas et al. 2006).

Field Survey. In September, 50 plants were chosen in five 50-m transects located throughout the study area (hereafter T1, T2, T3, T4, and T5). The number of spiders and flowers in anthesis were counted on each plant. In addition, we estimated foliage cover for each individual plant as an ellipse $(0.25\pi \times \text{major})$ branch spread \times minor branch spread). To explore the influence of plant exposure on the distribution of spiders, we also recorded the number of plants that were either exposed or growing under the canopy of a tree in each transect. The counts were repeated 1 mo later (October). Pearson correlations (r) were used to assess the relationship of total number of spiders with the total number of flowers in anthesis, foliage cover average, and total number of exposed plants across transects in September and October.

In addition, we used logistic regression analyses to test whether the number of flowers in anthesis and foliage cover explained the presence/absence of spiders among plants within each of the five transects. This approach was used because most plants within transects had either none or only one or two spiders, making the use of ordinary regression analysis unfeasible. Logistic regression is similar to ordinary regression except that the response variable (y) is binary (i.e., has only two possible qualitative outcomes) instead of continuous (Neter et al. 1996, Mendenhall and Sincich 2003). For each transect, the presence or absence of spiders on each plant (response variable) was coded as 1 or 0, respectively. The number of flowers in anthesis and foliage cover were included as predictor variables in each logistic regression model. The logistic regression parameters were obtained by maximum likelihood estimation (Mendenhall and Sincich 2003). The whole-model and regression parameters significance were tested using the likelihood ratio χ^2 test (Mendenhall and Sincich 2003).

Field Experiment. On 30 September, we conducted a field experiment to inspect the influence of inflorescences of C. ciliatoglandulifer on the spider distribution. Thirty individual plants with lynx spiders were randomly divided into two 15-plant groups. The first group was left untouched (controls, CO), whereas the second one was kept with no inflorescences during the course of the experiment (RI). Additionally, 15 individual plants without lvnx spiders were randomly selected. In this plant group, natural inflorescences were removed during the course of the experiment and substituted with artificial inflorescences that were similar to the natural ones (AI). If flowers are used as cues of prey availability, lynx spiders would colonize plants from which natural inflorescences were replaced by artificial flower heads and be as abundant as as on plants with natural inflorescences. A pilot trial showed that the total number of insects visiting control plants with natural inflorescences was significantly higher than plants with artificial inflorescences (t = 4.7, P < 0.001, df = 14). Moreover, the number of insects that were used as prey by P. viridans was also significantly higher in plants with natural inflorescences (t = 2.8, P < 0.005, df = 14). Both natural and artificial inflorescences had white actinomorphic 1.5to 2.0-cm flowers. Artificial racemes were 15 cm and had 12.6 \pm 1.2 flowers (mean \pm SE). Racemes of natural plants reached 15 cm and had 9.1 ± 2.2 flowers. Three artificial racemes were placed on each of the 15 plants in the AI treatment. Inflorescence removal from RI and AI treatments was done with minimum disturbance. To reduce the effect of other factors, not manipulated by the experimental treatments, all experimental plants had similar height and foliage cover and were under similar sun exposure conditions. To avoid contact between plants, experimental individuals were at least >1 m distant apart.

At the beginning of the experiment, the number of spiders on plants from which inflorescences were removed was higher than control plants (mean \pm SE: 2.4 ± 0.25 and 1.73 ± 0.21 spiders/plant, respectively); however, this difference was not significant (t = 2.035, P = 0.0514, df = 28). The number of spiders was counted on 30 September, 5 October, 14, 21, and 29, and 4 November, and 1 and 15 December. Flowers in anthesis were also counted on the same dates for the control plants. The effect of inflorescences on spider abundance was evaluated using a repeated-measures analysis of variance (ANOVA) with flower experimental treatment as the fixed effect and time as the repeated factor (von Ende 2001). To test our two hypotheses, we carried out two planned comparisons (Sokal and Rohlf 1995). First, if plants with natural inflorescences represent higher-quality patches than plants without inflorescences (CO versus RI), differences in spider abundance between CO and RI would

imply a difference in patch quality. Second, if inflorescences per se are used as cues of prey availability (CO versus AI), we would expect no difference between CO and AI. This would suggest that spiders use flowers as cues to select plants and not the potential prey that are more common on natural inflorescences (CO). This analysis did not include the first date because plants with artificial inflorescences (AI) had no spiders (30 September). Because the control plants (CO) had no inflorescences in the last two dates (1 December and 15) because of natural senescence and the differences between CO and RI ceased to be meaningful, we also removed the last date (15 December) from the analysis. The previous date (1 December) was included to be conservative and because there could still be flowers on previous days before the count. Before the analysis, the number of spiders was log(n + 1) transformed to normalize its error distribution (Sokal and Rohlf 1995) and to meet the assumptions of sphericity and equality of covariance matrices (von Ende 2001). All analyses were performed using the JMP (SAS Institute 1999) or NCSS (Hintze 2001) statistical packages.

Results

Field Survey. In September, the total number of spiders showed a positive relationship with average foliage cover and the number of exposed plants among transects; however, these correlations were not significant (r = 0.86, P = 0.06 and r = 0.87, P = 0.0543, respectively; n = 5; Fig. 1A and B). The number of spiders was not correlated with the number of flowers in anthesis in the same month (r = 0.02, P = 0.9786, n =5; Fig. 1C). However, in October, the number of spiders had a high positive correlation with the number of flowers in anthesis (r = 0.99, P = 0.0001, n = 5; Fig. 1C) but not with the number of exposed plants (r =-0.63, P = 0.2505, n = 5; Fig. 1B). We also found a negative but not statistically significant relationship between the number of spiders and foliage cover during this month (r = 0.87, P = 0.0545, n = 5; Fig. 1A).

Because foliage cover was never significant within transects (P > 0.09 in all cases), this plant attribute was dropped from the final logistic regression models. Within each transect, the simple logistic regression analyses showed that the probability of the presence of spiders increased with the number of flowers only in transect T3 in September (Table 1; Fig. 2A). In contrast, in October, the number of flowers explained the presence of spiders in four of the five transects (Table 1; Fig. 2B). In T4, the results were only marginally significant (Table 1). In all cases, the probability of spider presence increased with the number of flowers (Table 1; Fig. 2B). These results were consistent with the correlations analyses among transects. Spiders were more common on plants with flowers in October but not in September.

Field Experiment. Results from the experiments show that the number of spiders was significantly different between inflorescence treatments (F = 23.56, df = 2,42; P = 0.0373). In particular, plants with



Fig. 1. Relationship between the number of spiders and (A) average foliage cover, (B) number of exposed plants, and (C) number of flowers in anthesis, in five transects (n = 50 plants per transect) in a dry forest in western Mexico in September and October.

natural inflorescences (CO) had significantly more spiders than plants without natural inflorescences (CO versus RI planned comparison: F = 6.49, df = 1,42; P = 0.0146; Fig. 3A). However, there were no differences in spider abundance between plants with natural and artificial inflorescences (CO versus RA planned comparison: F = 3.82, df = 1,42; P = 0.0570; Fig. 3A). Although spider abundance varied signifi-

cantly over time (F = 6.34, df = 5,210; P < 0.0001), these differences were not significant between treatments (inflorescences treatment \times time interaction: F = 1.79, df = 10,210; P = 0.0633; Fig. 3A). However, separate within-subject repeated-measured analysis detected a significant increase in spider abundance over time in plants with artificial inflorescences (time effect: F = 5.60, df = 5,70; P = 0.0002). Plants with artificial inflorescences, originally with no spiders, were colonized from the first week after the treatments started (Fig. 3A). Spider abundance on plants with natural inflorescences removed (RI) decreased during the first 3 wk but increased during the fourth week, when there were almost no flowers left in the study area (Fig. 3A and B). There was a second blooming episode on 29 October (Fig. 3B). During this time, spider abundance once more diminished on plants without natural inflorescences (RI) and reached their highest abundance in both controls (CO) and plants with artificial inflorescences (AI; Fig. 3A). After this event, the flowering period declined and ceased in 1 December (Fig. 3B). Although plants from the three treatments had similar spider densities after 4 November, plants with artificial inflorescences had more spiders than the other two treatments in 15 December (Fig. 3A; date not included in the analysis). This difference, however, was not significant (F = 0.55, df = 2,42; P = 0.5821).

Discussion

The distribution of the green lynx spider P. viridans showed a close relationship with the number of flowers on C. ciliatoglandulifer. In addition, our experimental results suggested that the presence of inflorescences had a positive effect on spider abundance on the host plant. However, this relationship was not constant in time, and a trade-off between sun exposure and number of flowers may explain this inconsistency. Host plant choice is a dynamic process that might depend on available resources (i.e., flowers) and physical factors such as temperature, humidity, and light incidence (Cherrett 1964; Riechert and Tracy 1975; Romero and Vasconcellos-Neto 2004, 2005). In this study, the number of flowers had an important role in October, which followed the main blooming peak. In contrast, in September, when most inflorescences were in anthesis, plant exposure better explained the spider distribution.

Lynx spiders are strongly associated with plants bearing glandular trichomes (Vasconcellos-Neto et al. 2007), and *P. viridans* is almost only found on *C. ciliatoglandulifer* in our study area (Corcuera et al. 2008). Insects caught in resinous hairs might provide food for the spiders as suggested by Vansconcellos-Neto et al. (2007). However, we did not see insects trapped in *C. ciliatoglandulifer*, as we formerly pointed out. Moreover, a red-eyed seed chalcid wasp (Eurytomidae), frequently seen on the inflorescences, seemed to be intoxicated by the plant metabolites and, together with the honey bee (*Apis mellifera*), was one of the main prey of *P. viridans* (E. Jiménez-Salinas, unpub-

Month/transect	Whole-model test			Parameter estimate test ^a		
	χ^2_{1}	Р	R^2	$\beta_{\text{flowers}} (\text{SE})^b$	χ^2_1	Р
Sept.						
Ť1	1.81	0.1791	0.03	0.075(0.058)	1.64	0.2003
T2	0.53	0.4667	0.01	0.050(0.068)	0.55	0.4600
T3	27.06	0.0001	0.39	0.413 (0.118)	12.11	0.0005
T4	1.52	0.2175	0.03	0.034 (0.028)	1.48	0.2245
T5	0.36	0.5470	0.01	0.018 (0.030)	0.35	0.5539
Oct.						
T1	7.05	0.0079	0.10	0.193 (0.083)	5.38	0.0203
T2	12.95	0.0003	0.24	0.308 (0.117)	6.88	0.0087
T3	8.77	0.0030	0.17	0.241 (0.019)	4.89	0.0270
T4	5.58	0.0181	0.08	0.210 (0.104)	3.72	0.0537
T5	5.26	0.0218	0.08	0.120 (0.058)	4.16	0.0414

Table 1. Summary of the simple logistic regression analyses used to evaluate the effect of the no. of flowers on the spiders presence probability for each transect in Sept. and Oct.

^{*a*} Results of β_0 estimates are not shown.

^b Logistic regression coefficient to the effect of no. of flowers (SE).

 R^2 , proportion of the total uncertainty attributed to the model fit (SAS 1999).

lished data). Turner (1979) also found that *A. mellifera*, together with other Hymenoptera, was the main prey of *P. viridans* on a sagebrush in California.

Many foliage-dwelling spiders, such as *Peucetia* spp., prefer inflorescences to vegetative branches (de Souza and Martins 2004, de Souza and Módena 2004,



Fig. 2. Probability of spider occurrence in relation to number of flowers, fitted with a simple logistic regression model, in five transects (n = 50 plants per transect) in a dry forest in western Mexico in (A) September and (B) October 2007. T1–T5 refer to transect number. Significance of the logistic regression coefficients: *P = 0.0537; †P < 0.05; ‡P < 0.01; §P < 0.0001; NS, non significant.



Fig. 3. (A) Number of individuals of *P. viridans* on plants of *C. ciliatoglandulifer* with natural (\blacktriangle) and artificial (\Box) inflorescences and without inflorescences (\blacklozenge) in eight consecutive sampling dates. (B) Number of flowers of the control plants (natural inflorescences) during the same sampling dates. Error bars represent ± SE. Dates 30 September and 15 December were not included in the analysis (see the Field Experiment section in Material and Methods for details).

but see Morais-Filho and Romero 2008). Species of runners (Clubionidae and Anyphaenidae), ambushers (Thomisidae, Philodromidae, and Pisauridae), and stalkers (Salticidae and Oxyopidae) were more common on natural inflorescences than on nonreproductive branches of four plant species in the Brazilian pantanal (de Souza and Martins 2004). De Souza and Martins (2004) also found that stalkers were more abundant on artificial inflorescences than on vegetative branches. The positive relationship between P. viridans and flower number, as well as the diminishing abundances from plants from which the inflorescences were removed and a rise in spider numbers on plants with artificial flowers, highlight the importance of inflorescences on the distribution of P. viridian on its host plants. Nonetheless, the preference for flowering plant individuals does not seem to be the case for all lynx spiders. Morais-Filho and Romero (2008) found no differences in numbers of Peucetia flava Keyserling between hydrophitic shrubs of Rhyncanthera dichotoma (Nees) C.B. Clarke (Melastomataceae), with and without flowers. Instead, plant height,

number of leaves, and number of arthropods explained the distribution of this species.

De Souza and Módena (2004) suggested that, besides attracting potential prey, inflorescences add an architectural dimension to plants by modifying microclimatic conditions and providing refuges from predators. These authors found that Oxyopidae species were equally abundant among the three plants they studied, but individuals were significantly larger on one of the species with small flowers. Plants with larger flowers tend to be visited more frequently by insects but, in this case, spiders on these plants were also more vulnerable to bird predation. The preference for *C. ciliatoglandulifer* in our study area does not seem to be related to predation by birds because insectivorous species avoid *C. ciliatoglandulifer* and forage on other plants (Corcuera 2001).

Some flower dwelling spiders such as *Misumena* vatia (Clerck) (Thomisidae) actively respond to the insects attracted by plants (Morse 1988, 1999, 2000). Trichobothria and lyriform organs may detect prey from relatively large distances (Barth and Höller According to Arango et al. (2000), *P. viridans* is guided by color recognition and/or the amount of floral nectar in choosing individual plants. Even though insects can be attracted to artificial flowers (Bernays and Chapman 1994), we found that the total number of insects, as well as the preferred prey of the spider, was significantly higher on plants with natural flower heads. Because the spider was equally common on plants with artificial (once colonized) than natural inflorescences, our results agree with those of Arango et al. (2000) in the sense that *P. viridans* may be guided by color recognition. They also suggest that flowers per se are more important as cues for microhabitat selection than the amount of nectar and probably the presence of potential prey.

In addition to number of flowers and occurrence of inflorescences, plant exposure has been found to be related to the distribution of *P. viridans* (Arango et al. 2000, Romero and Vasconcellos-Neto 2004). Our results showed that flower choice was not constant in time. The relationship between the spider and number of flowers was significant, in all transects, only during October. However, spiders were present in plants with more flowers just in one of the five transects in September. The stimuli to choose a microhabitat (i.e., host plant) therefore are not invariable in time. In the dry, cold season, spiders showed no preference for flower heads (Romero and Vasconcellos-Neto 2004), whereas Arango et al. (2000) found that gravid females chose the more shaded plants, decreasing the probability of spiderling desiccation. In this study, we found more spiders on exposed plants during September when temperatures have already dropped with respect to the hottest months (April-May), and desiccation would be unlikely. Spiders might be more abundant in exposed sites because a higher radiation could stimulate its metabolism and, with no foliage interference, prey detection (either visual or vibratory) should be easier. In October (autumn), flower supply is drastically lower and spiders might have to become more selective. The flower/spider ratio was higher in late September (19.4) than in late October (5.3). Because flower supply was so much higher in the first case, spiders would not need to be selective and might choose sites with less interference represented by foliage to catch their prey.

In conclusion, our study confirms the positive effect of *C. ciliatoglandulifer* inflorescences on the distribution of *P. viridans*. Nevertheless, when flower availability is high, spiders seem to respond to plant exposure, either to optimize their thermoregulation or to detect prey without the interference of foliage. Furthermore, because spiders are equally common on plants with natural and artificial inflorescences, flowers are likely to be used as cues of prey availability instead of the visitors they attract.

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