

## ANTI-HERBIVORE PROTECTION BY MUTUALISTIC SPIDERS AND THE ROLE OF PLANT GLANDULAR TRICHOMES

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**Abstract.** Although specific associations between spiders and particular types of plants have been reported for several taxonomic groups, their consequences for spiders and plants are still poorly understood. The most common South American lynx spiders, *Peucetia flava* and *P. rubrolineata*, live strictly associated with various plant species that have glandular trichomes. To understand more about these spider–plant relationships, we investigated the influence of the spiders on the fitness of a neotropical glandular shrub (*Trichogoniopsis adenantha*) and on the arthropod community structure on the plant. We also tested whether glandular hairs provided any benefit to the spiders. Spiders reduced the abundance of several species and guilds of herbivores on the leaves and inflorescences. Consequently, damage to the leaves, capitula, ovaries, corollas, and stigmas caused by leaf-mining and chewing insects, as well as endophagous insects, were strongly reduced in the presence of *Peucetia* spp. Although the spiders fed on flower visitors, their negative influence on ovary fertilization was only marginally nonsignificant ( $P = 0.065$ ). Spiders on plants of *Trichogoniopsis adenantha* that fed on common fruit flies that had died before adhering to the glandular trichomes did not lose body mass. However, those living on plants without stalked glandular trichomes (*Melissa officinalis*) did not feed on dead flies and lost 13–20% of their biomass. These results indicate that *Peucetia* spiders are effective plant bodyguards and that when there is limited live prey they may feed on insect carcasses adhered to glandular trichomes. Since several spider species of the genus *Peucetia* live strictly associated with glandular trichome-bearing plants in neotropical, Nearctic, Palearctic, and Afrotropical regions, this type of facultative mutualism involving *Peucetia* and glandular plants may be common worldwide.

**Key words:** Asteraceae; cost/benefit analysis; glandular trichomes; mutualism; neotropical rain forest, southeastern Brazil; Oxyopidae; Peucetia; pollination; scavenging behavior; seed predation; top-down effects; *Trichogoniopsis adenantha*.

### INTRODUCTION

Plants have evolved diverse anti-herbivore defenses. Intrinsic defense mechanisms involving physical and chemical defenses can reduce plant damage by directly suppressing herbivores (Coley and Barone 1996, Stamp 2003), whereas extrinsic defenses involving biotic mechanisms can indirectly suppress herbivores via the third trophic level, i.e., by attracting predators or parasitoids that act as plant bodyguards (Price et al. 1980). The attraction and maintenance of mutualistic bodyguards on plants are typically mediated by infochemicals (synomones; De Moraes et al. 1998), food rewards such as food bodies and nectar from extrafloral nectaries, and/or shelter such as ant or leaf domatia (Heil and McKey 2003, Romero and Benson 2005). However, diverse plant morphological traits such as trichomes and plant architecture that apparently did not coevolve with predators can mediate mutualistic interactions between

predators and plants (Marquis and Whelan 1996). For example, although glandular trichomes have evolved as an intrinsic, mechanical plant defense against phytophages (Duffey 1986, Hare and Elle 2002), they can also promote arthropod–plant mutualisms (Ellis and Midgley 1996, Anderson and Midgley 2002, 2003, Romero and Vasconcellos-Neto 2004a, Anderson 2005).

Several predatory arthropods live specifically associated with plants bearing glandular trichomes where they capture prey adhered to these sticky structures (Dolling and Palmer 1991, Wheeler 2001, Romero and Vasconcellos-Neto 2003, Anderson 2006, Sugiura and Yamazaki 2006, Vasconcellos-Neto et al. 2007). Spiders are among the most common predators on glandular plants (Simon 1890, Lawrence 1964, Arango et al. 2000, Anderson and Midgley 2002, Romero and Vasconcellos-Neto 2004a, b, Vasconcellos-Neto et al. 2007). For instance, at least 10 lynx spider species of the genus *Peucetia* (Oxyopidae) live strictly associated with several plant species and families bearing glandular trichomes in many distinct vegetation types in neotropical, Nearctic, Palearctic, and Afrotropical regions (Vasconcellos-Neto

et al. 2007). Although these spider–plant systems are distributed worldwide, nothing is known about whether these interactions are mutualistic, i.e., whether the plants are protected by *Peucetia* against herbivores and whether glandular trichomes provide some benefit for the spiders, such as facilitating prey capture by trapping insects or preventing them from becoming dislodged and escaping (Vasconcellos-Neto et al. 2007).

To understand the relationship between *Peucetia* spiders and glandular plants better, we investigated the interaction between the two most common neotropical species, *Peucetia flava* and *P. rubrolineata*, and a neotropical shrub bearing glandular trichomes. Specifically, we assessed whether this spider–plant interaction was mutualistic, i.e., if glandular hairs provide any benefit to *Peucetia* spp., and if these spiders protect plants against herbivores. However, since *Peucetia* spiders typically feed on herbivores and on pollinators on their host plants (G. Q. Romero, J. C. Souza, and J. Vasconcellos-Neto, *personal observations*), their indirect effects on the plants can range from beneficial to harmful. We tested (1) whether *Peucetia* spp. influenced plant fitness (seed set) by removing phytophagous insects and/or pollinators from the host plant, (2) whether *Peucetia* spp. recognized and selected plants bearing glandular trichomes, and (3) whether these sticky structures improved spider growth.

## METHODS

### *Study area and organisms*

The experiments were done in 2006 (February–May) and 2007 (January–March) in a neotropical semi-deciduous forest at an elevation of 1000 m in the Ecological Reserve of the Serra do Japi (Leitão-Filho 1992) in southeastern Brazil (23°11' S, 46°52' W). The climate is seasonal, with a warm rainy season between November and April and a cooler dry season between June and September. The mean monthly temperatures vary from 13.5°C in July to 20.3°C in January (Pinto 1992).

*Trichogoniopsis adenantha* (DC) (Asteraceae) is a small perennial shrub that is abundant along submontane semi-deciduous forest margins in southeastern Brazil. The leaves and stems of this shrub bear glandular trichomes on which small insects (ants and chironomid midges) frequently become adhered (Romero and Vasconcellos-Neto 2003, 2004a, b, 2005a). For instance, ~90% of all ants and chironomid midges found on this plant species were adhered to these sticky structures (Romero and Vasconcellos-Neto 2003); each plant can have 1–5 incidental insects adhered to their glandular hairs (G. Q. Romero, *personal observation*). Capitula (inflorescences) are produced throughout the year, with a peak in the rainy season (January–April). Each capitulum contains ~40 whitish ovaries that turn black after fertilization. In greenhouses, where there are no floral visitors, achenes (dry fruits) are not produced, indicating that *T. adenantha* requires pollinators for

fertilization (Romero and Vasconcellos-Neto 2004a). The most common floral visitors of *T. adenantha* at the study site were ithomiine butterflies (*Pseudoscada erruca*, *Episcada carcinia*, *Aeria olena*; Nymphalidae), various species of ctenuchine moths (Arctiidae), honeybees, bumblebees (Apoidea), and syrphid flies (Romero and Vasconcellos-Neto 2004a, 2005a). The leaves of *T. adenantha* are frequently attacked by leaf-mining flies (especially Agromyzidae), by some chewing insects, such as a dark chewing Geometridae larvae (Geometridae sp. 1), a Pyralidae larvae, a black chrysomelid beetle, grasshoppers, sucking insects such as *Macrolophus aragarcanus* (Miridae), aphids, and other homopterans. Additionally, their capitula are typically attacked by a green chewing Geometridae larvae (Geometridae sp. 2), endophagous larvae of *Trupanea* sp. (Diptera, Tephritidae), and *Melanagromyza* sp. (Diptera, Agromyzidae) that feed on several ovaries, and the corolla gall-maker *Asphondylia* sp. (Diptera, Cecidomiidae) that feeds on a single corolla (Almeida 1997, Romero and Vasconcellos-Neto 2004a). The endophagous flies *Trupanea* and *Melanagromyza* are frequently parasitized by species of Braconidae and Pteromalidae (Hymenoptera; Romero and Vasconcellos-Neto 2004a).

At the study site, *T. adenantha* was frequently inhabited by the lynx spiders *Peucetia flava* (Fig. 1) and *P. rubrolineata* (Oxyopidae; Vasconcellos-Neto et al. 2007). These two spider species share similar size: adult females of *P. flava* and *P. rubrolineata* can reach 14.4 and 13.3 mm, respectively (Santos and Brescovit 2003). The foraging behavior of these two spider species is very similar and both feed on similar prey items that consist of a variety of insects, including phytophages (*Trupanea* sp., Geometridae sp. 1 and 2) and pollinivores/nectarivores (*Pseudoscada*, *Episcada*, *Aeria olena*, bees and wasps; G. Q. Romero, J. C. Souza, and J. Vasconcellos-Neto, *personal observations*). Apart from *Peucetia*, *T. adenantha* is also frequently inhabited by other smaller predators, such as the crab spider *Misumenops argenteus* (Thomisidae; Romero and Vasconcellos-Neto 2004a) and some reduviid bugs, e.g., *Bactrodes femoratus*.

### *Spider effects on the plants*

*Experimental design.*—The experiment to test the effects of *Peucetia* spp. on the number of arthropods, the rate of herbivory on leaves and flowers, and on ovary fertilization was done from 9 February to 19 May 2006 at the margins of a semi-deciduous forest close to natural populations of *T. adenantha*. Forty-two saplings of *T. adenantha*, 50–60 cm tall, were collected on 10–15 December 2005, and transplanted to pots 25 cm in diameter and 18 cm high containing homogeneous soil collected from the same place as the plants in order to minimize bottom-up interference. The potted plants were placed together in an area close to the Ecological Reserve to minimize arthropod colonization until the plants produced the first capitula. The plants were



FIG. 1. Adult female *Peucetia flava* on *Trichogoniopsis adenantha*'s capitula. Photo credit: G. Q. Romero.

subsequently transferred to the field along a wood edge and set out in pairs (totaling 21 pairs or blocks) according to their size (each block contained plants of similar height). A distance of 0.5–1.0 m separated paired plants, and each pair was located at least 2.5 m from conspecifics. One plant of each pair was randomly chosen to receive *Peucetia* spp. spiders (spider-presence treatment) while the other plant did not receive spiders (spider-absence treatment). Approximately a half of the plants of the spider presence treatment had *P. flava* and the remainder had *P. rubrolineata*; the two spider species used were randomized among the plants from the experiment. The number of spiders on each experimental plant was similar to the number of spiders on *T. adenantha* growing naturally in the field, which varied from one to three spiders according to the plant's size (G. Q. Romero, J. C. Souza, and J. Vasconcellos-Neto, *personal observations*). All plants were inspected daily and spiders were added or removed as necessary to maintain the treatments. The spiders were kept on the plants until maturation of the capitula (pre-dispersion phenophase, after 25–30 d of development; Romero and Vasconcellos-Neto 2005a).

*Number of arthropods, leaf and floral herbivory, and ovary fertilization.*—All arthropods, including chewing, sucking, and leaf-mining herbivores, as well as predators and insects that eventually landed on the plants, were counted weekly on the leaves, stems, and capitula, from 22 February to 5 April 2006. Damage to the leaves, i.e.,

proportion of leaves chewed and mined relative to the total number of leaves produced per plant, was recorded four times, from 10 February (pre-treatment samplings) to 29 March 2006.

To estimate floral herbivory and rate of ovary fertilization, all of the capitula in pre-dispersal phenophase on each experimental and control plant were collected from February to May 2006 and were stored separately in the laboratory in acrylic cups for a few days until the adult endophagous insects or their parasitoids had emerged. The capitula were then dissected and the number of fertilized and unfertilized ovaries, as well as damaged and intact ovaries or achenes (achenes are the dry fruits or fertilized ovaries) was recorded. Since each achene typically produced only one seed, the number of achenes (fruit set) was equal to the number of seeds (seed set; Salomão et al. 2006). Additionally, intact and damaged corollas and stigmas and the type of damage they suffered were also recorded. The number of endophages (puparia or adults) of each species and the number of hymenopterans (parasitoids) that emerged were counted. Since some capitula were heavily damaged by Geometridae sp. 2, which made the counting of achenes difficult, the number of achene (or ovarian) scars in the floral receptacle was used to estimate the number of achenes (or ovaries) produced.

*Statistical analyses.*—All statistical analyses were done using randomized-block analyses of variance (Underwood 1997) in which each plant pair was a block

(random effect) and each member of a block received a treatment (presence or absence of spiders; fixed effect). The effect of *Peucetia* spp. on the number of arthropods (chewers, suckers, predators, and eventuals) on the plants was compared using a repeated-measures, randomized-block ANCOVA in which time was the repeated factor and the mean number of leaves produced during the experiment was the covariate. The proportion of leaves damaged by chewers and leaf miners relative to the total number of leaves produced was compared between treatments by using repeated-measures, randomized-block ANCOVA, in which time was the repeated factor and the initial proportion of leaves chewed or mined (pre-treatment damage) was included as a covariate to control for differences in damage between groups at the beginning of the experiment. Separate analyses of variance were also done to assess the effect of the spiders on leaf damage in each group of data (including the pre-treatment). For the repeated measures containing more than two repeated factors, the *F* statistics and the probabilities were Greenhouse-Geisser (G-G) corrected for sphericity (Sokal and Rohlf 1995).

The total number of endophagous insects and the number of endophage taxa in the capitula were compared between treatments using randomized-block ANCOVAs in which the total number of capitula produced by the plant during the experiment was the covariate. The proportion of capitula infested by endophagous (e.g., *Trupanea*, *Melanagromyza*) and exophagous (Geometridae sp. 2) insects relative to the total number of capitula produced per plant was compared using a randomized-block ANOVA. The proportions of ovaries (or achenes) damaged by these herbivores were compared using randomized-block ANCOVA, with the total number of capitula as the covariate. The latter general linear model was also used to compare the proportion of corollas damaged and the proportion of corollas that lacked stigmas relative to the total number of open corollas in the two treatments. In the analysis of ovaries damaged by each herbivore separately, the data for capitula with interspecific co-occurrence were not considered because it was not possible to estimate the exact number of ovaries damaged by each herbivore species. Randomized-block, repeated-measures ANCOVA was used to test the effects of *Peucetia* spp. and capitula condition (infested vs. uninfested) on the proportion of intact, fertile ovaries (viable achenes). The proportion of viable achenes was calculated as the total number of undamaged fertilized ovaries divided by the total number of undamaged ovaries (fertilized + unfertilized) produced in each capitulum. The total number of capitula per plant was the covariate and capitula condition was the repeated factor (within subjects analysis; random factor). The parameters "uninfested capitula" and "infested capitula" tested for, respectively, "direct effects" (effect of the spiders alone) and "indirect effects" (complex interac-

tions between spiders and floral herbivores) on ovary fertilization.

Prior to the analyses, the data for abundance or density were  $\log_{10}(n + 1)$ -transformed, and the data for proportions were arcsine square-root transformed to normalize the distributions and obtain homogenous variances (Sokal and Rohlf 1995). All analyses of variance were run using Type III sums of squares (SS) and were done using GLM statistics. The mean values ( $\pm 1$  SE) were computed directly from untransformed data.

#### *Host-plant selection and the influence of glandular hairs on spider growth*

*Host-plant selection.*—To test whether *P. flava* and *P. rubrolineata* recognized and selected host plants with glandular hairs, 20 potted plants of *T. adenantha*, *Lantana camara* (Verbenaceae), and *Melissa officinalis* (Lamiaceae) of similar height and number of leaves were grouped in blocks at the edge of a semi-deciduous forest; each block consisted of one individual of each plant species. A distance of 0.3 m separated plants within each block, and the blocks were at least 2 m apart. Each plant in a block received one fifth or sixth instar individual of *P. flava* ( $n = 10$  blocks) or *P. rubrolineata* ( $n = 10$  blocks), and the total time the spiders spent on the plant was recorded. While *L. camara* does not bear glandular trichomes, the epidermis of *M. officinalis* is covered with numerous saccate oil glands; however, these glands are not on stalks as those in *T. adenantha* and apparently do not catch insects (G. Q. Romero, *personal observation*).

The plants *L. camara* and *M. officinalis* were used in this experiment because their architecture, leaf size, shape, and texture were similar to those of *T. adenantha*. *M. officinalis* and *L. camara* have repellent compounds against insects that could have an influence on the definite conclusions about host plant selection by *Peucetia* spp. Thus, we conducted a preliminary bioassay to test for this assumption by using 60 potted plants of *T. adenantha* grouped in blocks of three plants per block, using the same design and conditions as in the previous experiment. Each plant of the block was randomly chosen to be sprayed with aqueous extract (10 mL per plant) of *T. adenantha*, *L. camara*, or *M. officinalis*. Leaf extracts were obtained by macerating 5 g of fresh leaves in 100 mL of distilled water. Two minutes after the spray, each plant in a block received one fifth or sixth instar individual of *P. flava* ( $n = 10$  blocks) or *P. rubrolineata* ( $n = 10$  blocks), and the total time the spiders spent on the plant was recorded. The time spent by *P. flava* and *P. rubrolineata* on each experimental plant did not differ statistically (Kruskal-Wallis: *P. flava*,  $U = 2.79$ ,  $P = 0.247$ ; *P. rubrolineata*,  $U = 0.13$ ,  $P = 0.939$ ).

*Spider growth.*—Stalked glandular trichomes in *T. adenantha* frequently trap and kill small insects such as chironomid midges and ants, and this food source may be scavenged by *Peucetia*. To test whether small, dead

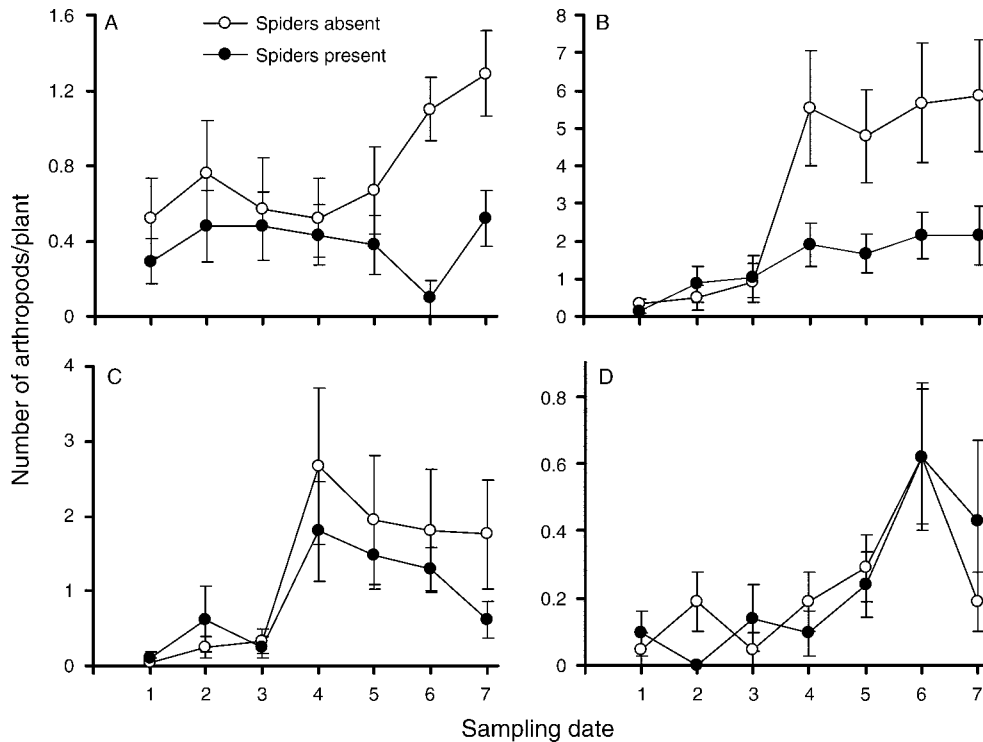


FIG. 2. Mean number of (A) chewers, (B) suckers, (C) other predators, and (D) insects that occurred occasionally on *Trichogoniopsis* plants in the absence (open circles) and presence (solid circles) of spiders. Error bars represent  $\pm 1$  SE. Sampling dates: 1 = 22 February; 2 = 1 March; 3 = 8 March; 4 = 15 March; 5 = 22 March; 6 = 29 March; and 7 = 5 April.

insects trapped by glandular hairs of *T. adenantha* were used as food by *Peucetia* spp., and whether these carcasses improved spider growth (increased biomass), an experiment was done using *T. adenantha* plants ( $n = 10$ ) and *M. officinalis* plants ( $n = 10$ ), which have simple trichomes but that lack the stalked glandular structures. Each plant was included in a cage lined with a fine mesh, and one fifth or sixth instar individual of *P. flava* or *P. rubrolineata* was placed on each caged plant. A short distance (5–15 cm) separated the mesh from the plants, thereby facilitating the migration of the spiders from the plants to the mesh and vice-versa. The spiders were collected from *T. adenantha* plants growing naturally and initially maintained in polyethylene pots (4.5 cm diameter, 5.0 cm high) with *Drosophila melanogaster* flies offered ad libitum for three days. In the following two days, the spiders were deprived of food, weighed on an analytical balance (precision of  $10^{-4}$  g) and then randomly transferred to the caged plants. Eight *D. melanogaster* flies were added to each *T. adenantha* and *M. officinalis* plants each day. The flies were killed (by freezing) and then distributed amongst both new and old leaves. After six days on the plants, the spiders were weighed again. The difference in mass between the first and second measurements was used as an indicator of each spider's growth rate. The feeding behavior of the spiders and the time spent on the plants were recorded.

## RESULTS

### Spider effects on the plants

*Number of arthropods and damage to the leaves.*—The number of chewing phytophagous insects (Geometridae sp. 1, Pyralidae sp., grasshoppers, Chrysomelid beetles) on the leaves and stems was lower on plants with spiders (randomized-block, repeated-measures ANCOVA,  $F_{1,19} = 6.96$ ,  $P = 0.016$ ; Fig. 2A). The interaction term between treatment and time was also significant ( $F_{6,114} = 3.69$ ,  $P = 0.007$ , after Greenhouse-Geisser (G-G) correction for sphericity). Similarly, the sucking phytophagous insects (*Macrolophus aragarcanus* and homopterans) decreased in the presence of *Peucetia* ( $F_{1,19} = 45.28$ ,  $P < 0.0001$ ; Fig. 2B), with the interaction term between treatment and time also being significant ( $F_{6,114} = 6.44$ ,  $P = 0.001$ , after G-G correction for sphericity). In contrast, the number of predators (reduviid bugs, ants, and other smaller spiders) and of insects that eventually occupied the plants (chironomids and other flies) did not differ between the groups (randomized-block, repeated-measures ANCOVA,  $P \geq 0.75$ ; Fig. 2C, D).

The number of leaves and stems increased significantly during the experiment (randomized-block, repeated-measures ANOVA,  $F_{3,60} \geq 126$ ,  $P < 0.0001$ ), but did not differ between the groups ( $F_{1,20} \leq 0.06$ ,  $P \geq 0.82$ ). The proportion of leaves damaged by leaf-mining insects relative to the total number of leaves produced tended to

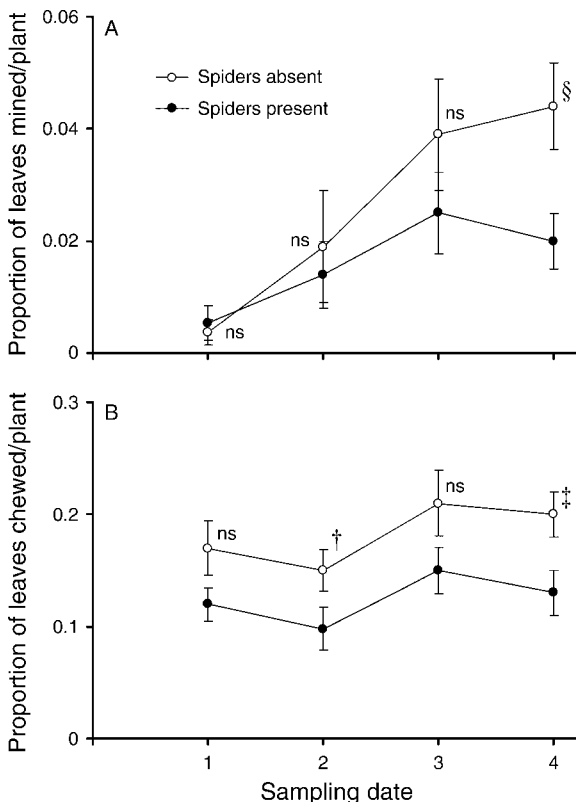


FIG. 3. Mean proportion of leaves damaged by (A) leaf mining insects and (B) chewing phytophagous insects relative to the total number of leaves on *Trichogoniopsis* plants in the absence (open circles) and presence (solid circles) of spiders. Error bars represent  $\pm$ SE. Sampling dates: 1 = 10 February (pre-treatment); 2 = 1 March; 3 = 15 March; and 4 = 29 March. Nonsignificant differences are indicated by "ns."

† $P = 0.041$ .  
‡ $P = 0.010$ .  
§ $P = 0.006$ .

decrease in the presence of spiders (Fig. 3A), but the difference was not significant (randomized-block, repeated-measures ANCOVA,  $F_{1,19} = 4.02$ ,  $P = 0.060$ ). The interaction term between time and treatment did not differ significantly ( $F_{2,38} = 1.94$ ,  $P = 0.167$ , after G-G correction for sphericity). However, separate analysis of variance detected a significant increase in the proportion of mined leaves in the absence of spiders in the last sampling period ( $P = 0.006$ ; Fig. 3A). There was also a marginally significant difference for the proportion of chewed leaves between plants with and without spiders ( $F_{1,19} = 4.11$ ,  $P = 0.057$ ). Again, the interaction term between time and treatment did not differ significantly ( $F_{2,38} = 0.23$ ,  $P = 0.763$ , after G-G correction for sphericity), but separate ANOVAs detected significant differences in the second ( $P = 0.041$ ) and fourth ( $P = 0.010$ ) sampling periods (Fig. 3B).

*Number of endophages and floral herbivory.*—The total number of herbivores (endophagous insects) within capitula did not differ significantly between the groups

(randomized-block ANCOVA,  $F_{1,19} = 0.45$ ,  $P = 0.510$ ; Fig. 4A). While the abundance of the endophage *Trupanea* sp. decreased  $\sim 1.5$  fold in the presence of *Peuceetia* ( $F_{1,19} = 7.60$ ,  $P = 0.013$ ), the abundance of *Melanagromyza* sp. did not differ significantly between the groups ( $F_{1,19} = 2.40$ ,  $P = 0.138$ ; Fig. 4A). The abundance of the corolla gall-maker *Asphondylia* sp. was similar in the two groups ( $F_{1,19} = 0.08$ ,  $P = 0.778$ ; Fig. 4A). The proportion of endophage parasitoids (Pteromalidae sp. and Braconidae sp.) relative to the total number of endophages (*Trupanea* + *Melanagromyza*) did not differ between the groups (Pteromalidae, spiders absent,  $0.32 \pm 0.04$ ; spiders present,  $0.24 \pm 0.04$ ; randomized-block ANCOVA,  $F_{1,19} = 1.32$ ,  $P = 0.265$ ; Braconidae, spiders absent,  $0.07 \pm 0.01$ ; spiders present,  $0.12 \pm 0.03$ ;  $F_{1,19} = 1.68$ ,  $P = 0.211$  [mean  $\pm$  SE]), indicating that intra-guild predation in this system was weak.

The total number of capitula produced by plants in the absence ( $19.9 \pm 5.3$ ; all data shown here are mean  $\pm$  SE) and presence ( $18.7 \pm 4.3$ ) of *Peuceetia* did not differ

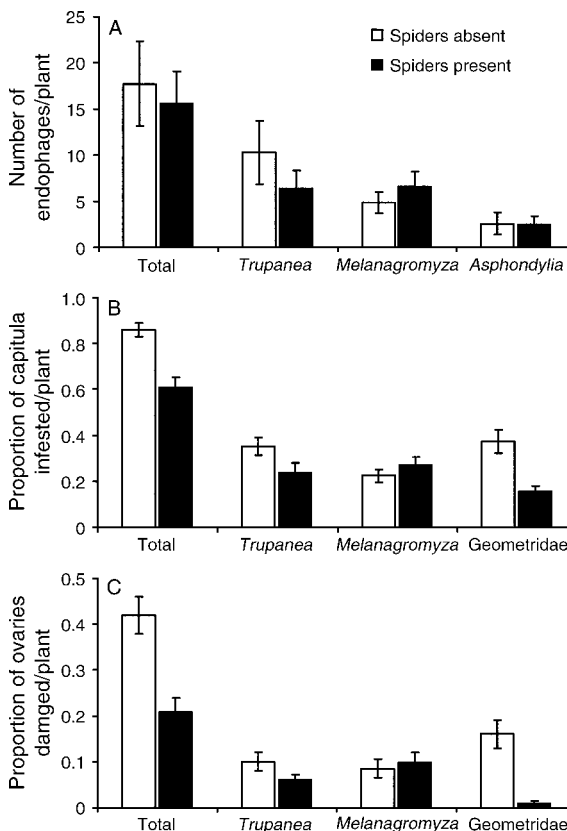


FIG. 4. (A) Mean number of endophages, (B) mean proportion of capitula infested (infested/total produced per plant), and (C) mean number of ovaries damaged (damaged/total produced per plant) by endophages (*Trupanea* sp., *Melanagromyza* sp., and *Asphondylia* sp.) and exophages (*Geometridae* sp. 2) on *Trichogoniopsis* plants in the absence (open bars) and presence (solid bars) of *Peuceetia*. Error bars represent  $\pm$ SE.

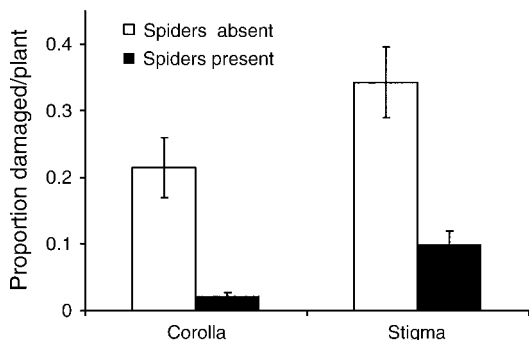


FIG. 5. Proportions of damaged corollas ("Corolla") and of corollas that lacked stigmas ("Stigma") relative to the total number of open corollas per plant of *Trichogoniopsis* in the absence (open bars) and presence (solid bars) of *Peucetia*. Error bars represent  $\pm$ SE.

significantly (randomized-block ANOVA,  $F_{1,20} = 0.23$ ,  $P = 0.640$ ). Similarly, there was no significant difference in the total number of ovaries produced by plants with ( $741.9 \pm 207.7$ ) and without ( $748.6 \pm 230.4$ ) spiders ( $F_{1,20} = 0.354$ ,  $P = 0.558$ ). The proportion of capitula infested by herbivores (endophages + exophages) relative to the total number of capitula produced decreased by a factor of 1.4 in the presence of *Peucetia* (randomized-block ANOVA,  $F_{1,20} = 24.44$ ,  $P < 0.001$ ; Fig. 4B). The proportion of capitula infested by *Melanagromyza* sp. did not differ significantly between the groups ( $F_{1,20} = 0.35$ ,  $P = 0.560$ ). In contrast, plants without spiders had a higher proportion of capitula infested by *Trupanea* sp. ( $F_{1,20} = 6.82$ ,  $P = 0.017$ ) and Geometridae sp. 2 ( $F_{1,20} = 19.01$ ,  $P < 0.001$ ) than plants with spiders (Fig. 4B). Consequently, the proportion of ovaries damaged by herbivores relative to the total number of ovaries produced was two-fold higher in the absence of spiders than in their presence (randomized-block ANCOVA,  $F_{1,19} = 21.93$ ,  $P < 0.001$ ; Fig. 4C). While the proportion of ovaries damaged by *Melanagromyza* sp. did not differ between the groups ( $F_{1,19} = 1.38$ ,  $P = 0.255$ ), the proportion of ovaries damaged by *Trupanea* sp. and Geometridae sp. 2 was, respectively, 1.6-fold and 16-fold higher in plants without spiders than with spiders (*Trupanea*,  $F_{1,19} = 6.76$ ,  $P = 0.018$ ; Geometridae,  $F_{1,19} = 32.13$ ,  $P < 0.001$ ; Fig. 4C).

The proportion of corollas damaged (especially by Geometridae sp. 2) relative to the total number of open corollas decreased in the presence of spiders (randomized-block ANCOVA,  $F_{1,19} = 18.76$ ,  $P < 0.001$ ). Similar results were also observed for the proportion of corollas that lacked stigmas relative to the total number of corollas ( $F_{1,19} = 14.11$ ,  $P = 0.001$ ; Fig. 5).

**Ovary fertilization and the cost/benefit effect of spiders to the plant.**—The *Peucetia* species preyed on several groups of flower visitors, including *Pseudoscada erruca*, *Aeria olena*, *Episcada carcinia* (Ithomiinae), Ctenuchinae moths, syrphid flies, and a variety of wasps and bees. Despite this predation, the negative effect of the spiders

on the proportion of fertilized ovaries in unfested capitula (direct effect) was nonsignificant (randomized-block ANCOVA,  $F_{1,12} = 4.12$ ,  $P = 0.065$ ; Fig. 6). The spiders had no effect on the proportion of fertilized ovaries in infested capitula (indirect effect; randomized-block ANCOVA,  $F_{1,12} = 2.14$ ,  $P = 0.169$ ; Fig. 6). Using capitula condition (infested vs. unfested) in a repeated-measures (within subjects) analysis of variance, the proportion of fertilized ovaries from infested capitula decreased significantly compared to that of fertilized ovaries from unfested capitula (repeated-measures, randomized-block ANCOVA,  $F_{1,12} = 6.59$ ,  $P = 0.025$ ; Fig. 6), indicating that floral herbivory affected plant fitness. However, the interaction term between capitula condition and treatment (spiders absent vs. present) was not significant (repeated-measures, randomized-block ANCOVA,  $F_{1,12} = 4.15$ ,  $P = 0.064$ ; Fig. 6).

#### Host-plant selection and spider growth

**Host-plant selection.**—The spiders *P. flava* and *P. rubrolineata* generally spent more time on their host plant (*T. adenantha*) than on other plant species that lacked stalked glandular structures (Fig. 7A). Whereas *P. flava* spent a similar time on *T. adenantha* and *L. camara*, but less on *M. officinalis* (Fig. 7A; randomized-block ANOVA,  $F_{2,18} = 5.56$ ,  $P = 0.013$ ), *P. rubrolineata* remained on their host plant for a total time of  $\sim 60$  hr on average, but spent much less time on the other plant species (Fig. 7A; randomized-block ANOVA,  $F_{2,18} = 4.50$ ,  $P = 0.025$ ).

**Spider growth.**—During the experiment with dead *Drosophila*, individuals of *P. flava* and *P. rubrolineata* were frequently seen feeding on the flies and scavenging for up to 20 hr after introduction of the flies. On the glandular plant *T. adenantha*, *P. flava* lost (4%) and *P. rubrolineata* gained (7%) body mass. However, when on plants that lacked stalked glandular hairs (*M. officinalis*), *P. flava* and *P. rubrolineata* lost 20% and 13% of their body mass, respectively (Fig. 7B). There was a significant difference in spider body mass between cages containing plants with and without glandular hairs, and

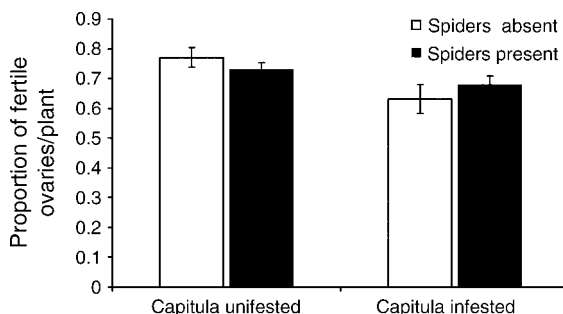


FIG. 6. Proportion of intact fertile ovaries relative to the total number of intact ovaries (fertile + unfertile) in unfested and infested capitula of *Trichogoniopsis* plants in the absence (open bars) and presence (solid bars) of *Peucetia*. Error bars represent  $\pm$ SE.

this difference was observed for *P. flava* ( $t$  test,  $t = 2.47$ ,  $df = 8$ ,  $P = 0.039$ ) and *P. rubrolineata* ( $t = 2.33$ ,  $df = 8$ ,  $P = 0.048$ ). This probably occurred because the spiders in cages with *T. adenantha* remained on the plant for long periods and fed on several fly carcasses adhered to the glandular trichomes; those that left *T. adenantha* returned to their host plant within a short time. In contrast, spiders in cages with *M. officinalis* remained in the mesh, were seldom observed on the plant, and fed on few fly carcasses; some flies may have fallen off of the *M. officinalis* leaves before the spiders could find them.

## DISCUSSION

### *Spider effects on the plants*

The lynx spiders *Peucetia* spp. reduced the abundance of several herbivorous species on the host plant, including chewers (beetles, lepidopteran larvae), suckers (homopterans, mirids), and endophages (miners and seed eaters, flies), and this reduced the types and extent of plant damage. The spiders' success in suppressing diverse guilds and species of herbivores may be related to their nonspecialist or broad diet. Indeed, spiders are typically generalists (Riechert and Lockley 1984), with *Peucetia* spiders being considered extreme generalists (Nyffeler et al. 1987). Generalist predators commonly engage in intraguild predation (Rosenheim 1998), feeding not only on phytophages, but also on other predators and parasitoids. Consequently, their influence on the food web may be variable, with disruptive effects for their host plant. However, since *Peucetia* did not significantly influence the abundance of other predators and parasitoids on the plant, intraguild predation in this system may be weak, and the combined effects of *Peucetia* and other natural enemies on phytophage suppression may be additive in this system.

*Peucetia* spp. decreased the density of the endophage *Trupanea* sp. and the exophage Geometridae sp. 2, the main seed (or ovary) eaters, but did not suppress the endophage *Melanagromyza* sp. or the corolla gall-maker *Asphondylia* sp. The taxon-specific influence of *Peucetia* can be explained by variation in the vulnerability of the phytophages: whereas *Trupanea* sp. females spent 29 min in egg laying and walked 19 cm on the plant, *Melanagromyza* sp. spent 16 min in egg laying and walked only 2.9 cm on the plant during this activity (mean values; Romero and Vasconcellos-Neto 2004a). Since Geometrid larvae are sessile, their vulnerability is greatly increased. Indeed, this moth was the herbivore most affected by *Peucetia*; with the proportion of damaged ovaries for this herbivore being 16-fold higher in plants without spiders than in those with spiders. Intriguingly, the influence of *Peucetia* spp. on the pattern of herbivore suppression was very similar to that of *Misumenops argenteus* (Thomisidae), another spider species that co-exists with the former spiders on *T. adenantha* (Romero and Vasconcellos-Neto 2004a). Although *Misumenops* and *Peucetia* differ in body size (the former genus is smaller than the latter) and hunting

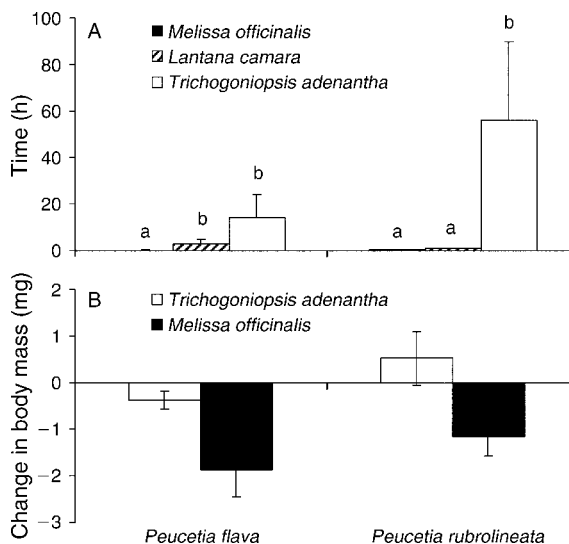


FIG. 7. Host plant selection and spider growth. (A) The duration of permanence of *P. flava* and *P. rubrolineata* on plants with (*T. adenantha*) and without (*M. officinalis* and *L. camara*) glandular trichomes, and (B) the net gain or loss of body mass by *Peucetia* spiders on *T. adenantha* and *M. officinalis*. Different letters indicate significant differences (Fisher LSD post hoc test,  $\alpha = 0.05$ ). Error bars represent  $\pm$ SE.

modes (the former forages as a typical sit-and-wait predator, while the latter forages more actively), they reduced the abundance and/or damage caused by Geometridae sp. 2 and *Trupanea* sp. to similar extents, but did not influence the abundance and damage caused by *Melanagromyza* sp. and *Asphondylia* sp. The redundancy in the ecological functions of these predators in this food web probably arose because the taxa that were suppressed were similarly vulnerable to both types of predators.

The suppression of herbivores by *Peucetia* spp. resulted in an increase in plant fitness. This finding agrees with other studies indicating that spiders can suppress herbivores and indirectly improve plant fitness (Louda 1982b, Rühren and Handel 1999, Romero and Vasconcellos-Neto 2004a, Whitney 2004 and references therein). Overall, *Peucetia* spiders decreased the damage to corollas, stigmas, and ovaries (or seeds) although, as expected, herbivore suppression was taxon specific. Several studies have shown that endophagous herbivores of Asteraceae may negatively influence the survival and recruitment of their native host plants (Louda 1982a, Louda and Potvin 1995) and that endophages may be suitable agents for the biological control of invasive or native Asteraceae (reviewed in Louda et al. 2003).

The beneficial effect of *Peucetia* on plant fitness could potentially improve host plant recruitment. However, when spiders are on flowers, they may prove costly for plants because of predation on potential pollinator insects (Dukas 2001, Dukas and Morse 2003, Suttle 2003, Heiling and Herberstein 2004, Robertson and



Klemash Maguire 2005). Indeed, *Peucetia* tended to decrease the proportion of fertilized ovaries in *T. adenantha*. Although this tendency was marginally nonsignificant ( $P = 0.065$ ), the presence of these spiders may result in some potential cost to the host plant. Louda (1982b) reported a significant negative effect of *Peucetia viridans* on the ovary fertilization of its host plant (*Haplopappus venetus*, Asteraceae). In this case, in addition to reducing phytophage abundance, *P. viridans* also decreased ovary fertilization by one-third. However, our results showed that the presence of *P. flava* and *P. rubrolineata* was clearly more beneficial than harmful for *T. adenantha*. Since these spider species live on many other glandular plant species in South America (Vasconcellos-Neto et al. 2007), they may affect their host plants in ways different from those reported here.

Whereas *Peucetia* spp. tended to decrease the proportion of fertilized ovaries in uninfested capitula (direct effect), with no effect on infested capitula (indirect effect), *M. argenteus* increased the proportion of ovary fertilization in infested capitula but had no effect on the uninfested capitula of *T. adenantha* (Romero and Vasconcellos-Neto 2004a). These contrasting effects may be explained by differences in foraging behavior combined with plant architecture. When on reproductive branches, *Peucetia* spp. frequently join the capitula in anthesis phenophase with silk and forage on them (see Fig. 1), thereby impeding pollinators from reaching the flowers. In contrast, *M. argenteus* limits itself to foraging only on a single capitulum, leaving the remaining capitula free to be visited by pollinators; the distance among capitula during anthesis (i.e., plant architecture) apparently hampers crab spiders preying on pollinators. Although recent work has stressed the importance of the integrative effects of predators on animal-plant mutualisms (Knight et al. 2006), the factors and mechanisms driving disruption in mutualistic interactions are still poorly understood. As shown here, variations in the effects of different flower-dwelling predators and in plant architecture were important determinants of plant reproductive output.

#### *Host-plant selection and spider growth*

*Peucetia* generally remained longer on *T. adenantha* than on plant species that lacked stalked glandular trichomes. This finding indicated that these spiders recognized and selected plants bearing this type of glandular hair. The specialization of *Peucetia* for a specific plant trait may have evolved because of the plant's stickiness (Vasconcellos-Neto et al. 2007), since glandular trichomes frequently trap and sometimes kill arthropods (Sugiura and Yamazaki 2006) that can be used by the spiders. Indeed, *Peucetia* frequently scavenged fly carcasses adhered to their host plant (as mentioned previously). The carcasses of dead prey provide an easily accessible food source without incurring the additional costs associated with attacking and manipulating live prey.

Although some plant-living spiders can evaluate the physical structure of their microhabitat in detail (Romero and Vasconcellos-Neto 2005b), the influence of the host plant on spider fitness is poorly understood. By selecting plants with sticky trichomes, *Peucetia* had access to fly carcasses on plant leaves and their body mass increased (*P. rubrolineata*) or decreased only slightly (*P. flava*). Although growth rate is only an indirect measure of animal fitness, it is reasonable to assume that the observed body mass increment may translate into a higher fitness for *Peucetia* spp. In contrast, spiders in cages with plants that lacked sticky trichomes did not eat dead flies, and consequently lost body mass. Sugiura and Yamazaki (2006) also observed an enhanced growth rate in the plant bug *Orthotylus gotoi* (Miridae) when fed insect carcasses. In periods of low prey abundance, the spiders on glandular plants may have access to decaying food and therefore survive for longer. These results suggest that the scavenging behavior of *Peucetia* associated with the gain in spider growth and fitness achieved by feeding on dead insects may have contributed to the evolution of host plant specialization.

#### *Mutualism between spiders and plants*

Our data show that glandular trichomes mediate facultative mutualism between *T. adenantha* and *Peucetia*. Although glandular trichomes in this species frequently trap and kill small insects (chironomid midges and ants) that may be used by the spiders, curiously these sticky structures only rarely trapped phytophagous insects (aphids); even insects not specific to this plant species, e.g., treehoppers and other homopterans, were not trapped or killed by the plant (G. Q. Romero, J. C. Souza, and J. Vasconcellos-Neto, *personal observations*). Glandular hairs on the leaves and stems of *T. adenantha* have likely evolved as an intrinsic, direct defense against herbivores, but their current function seems to be restricted to indirect defense, i.e., the attraction of *Peucetia* as plant bodyguards. Other studies have also reported that glandular hairs mediate arthropod-plant mutualisms. For instance, glandular hairs in carnivorous plants of the genus *Roridula* (Roridulaceae) contribute to the interaction with mutualistic plant bugs of the genus *Pameridea* (Miridae; Ellis and Midgley 1996, Anderson and Midgley 2002, 2003, Anderson 2005). These predatory insects feed on arthropods that adhere to the trichomes and also defecate on the plant, with up to 70% of all the nitrogen used by these plants being derived from mirids.

Spiders have a positive effect on plants by removing herbivores (Romero and Vasconcellos-Neto 2004a) and by improving plant nutrition and growth (Romero et al. 2006); conversely, plants can improve spider fitness (Smith and Mommsen 1984). However, very few studies have reported a positive reciprocal relationship between spiders and plants. Whitney (2004) stated that this lack of studies on spider-plant mutualisms is explained by

the generalized diet of spiders, which feed on herbivores but also on pollinators and third trophic level organisms (intraguild predation); such behavior reduces the effectiveness of spiders as plant bodyguards. However, our data suggest an alternative explanation, namely that for pairwise mutualisms between spiders and plants to be established, the spiders need to be spatiotemporally and closely associated with a particular plant species or at least a plant type, such as the association of *Peucetia* with glandular plants. However, little attention has been paid to the importance of specificity in spider–plant interactions. Consequently, the first step in understanding any mutualism between spiders and plants is to identify the plant morphological traits that improve spider fidelity in the association. To date, the best known examples of botanical structures that potentially increase spider fidelity to their host plants are leaves organized in a rosette shape (e.g., Bromeliaceae; reviewed in Romero 2006) and plant glandular trichomes (reviewed in Vasconcellos-Neto et al. 2007). These structures provide suitable systems for investigating spider–plant mutualisms.

In conclusion, our results have shed new light on the mutualistic relationship between *Peucetia* spiders and glandular plants. Since several spiders of this genus are associated with numerous glandular plant species worldwide (Vasconcellos-Neto et al. 2007), these spider–plant associations could provide suitable systems for investigating other mutualistic relationships. Identification of the plant traits that attract particular spiders will also improve our understanding of spider–plant mutualisms.

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