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Associations of Spiders of the Genus *Peucetia* (Oxyopidae) with Plants Bearing Glandular Hairs

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ABSTRACT

Two common South American species of lynx spiders, *Peucetia rubrolineata* and *P. flava* (Oxyopidae), were surveyed on three localities in southeastern Brazil to determine plant choice. Both species were found to be associated with plants bearing glandular trichomes. A literature review and complementary data show that ten *Peucetia* species are associated with up to 55 plant species bearing glandular trichomes in at least 20 distinct vegetation types (phytophysiognomies) in more than 36 localities in the Neotropical, Neartic, Afrotropical, and Paleartic regions. The main plant families used by the spiders were Solanaceae, Asteraceae, and Melastomataceae. The specialization of the *Peucetia* species for plants bearing glandular trichomes may have evolved because insects adhered to these sticky structures may be used as prey by the spiders.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: evolution; foraging; host plant specificity; lynx spider; specific associations.

SPIDERS ARE AMONG THE MOST ABUNDANT AND DIVERSE ARTHROPODS ON VEGETATION (Foelix 1996). Studies showed that spiders can evaluate, in fine details, the physical structure of plants (Romero & Vasconcellos-Neto 2005), enabling them to select plant microhabitats of better quality, like flowers or reproductive branches (Morse & Fritz 1982, Morse 1993, Greco & Kevan 1994). Typically, strict associations of spiders with particular plant types or species have been considered to be unusual, although recently a growing number of studies have shown that host-specificity in spider–plant systems may be more common than previously thought (*e.g.,* Romero 2006). For instance, nine species of jumping spider (Salticidae) have been reported to occur strictly on the Bromeliaceae (Romero 2006). In addition, some spiders (*e.g., Misumenops argenteus*, Thomisidae) were reported to forage on plants with glandular trichomes because these structures trap insects, which can be captured by the spiders (Romero & Vasconcellos-Neto 2003, 2004a). Although glandular hairs have probably evolved as a defense against herbivores and pathogenic fungi (Levin 1973, Duffey 1986), they can also mediate mutualistic interactions between plants and spiders or other predators (Dolling & Palmer 1991, Romero & Vasconcellos-Neto 2004c).

Specific associations between spiders and plants occur because plants have morphological traits (*e.g.,* rosette in Bromeliaceae and glandular trichomes in several plant groups) that provide suitable foraging, mating, and egg-laying sites to the spiders, shelter for adults and immatures, and nurseries for spiderlings (Romero & Vasconcellos-Neto 2005), thereby improving the fidelity of the spiders to live on them. Most spider–plant associations are reported in the Neotropical regions (Figueira & Vasconcellos-Neto 1991, Barth *et al.* 1988, Dias & Brescovit 2004, Romero 2006), although it seems likely that many as yet undescribed associations involving these organisms exist in other tropical and temperate regions. Simon (1890) was probably the first to report an association between spiders and plants among lynx spiders of the genus *Peucetia* (Oxyopidae) with plants bearing glandular trichomes in Yemen, Egypt, and Spain.

The spider genus *Peucetia* comprises 43 species with a worldwide distribution (Van Niekerk & Dippenaar-Schoeman 1994, Santos & Brescovit 2003, Platnick 2006). Besides being relatively common foliage dwelling spiders, little is known about the natural history of most species. Knowledge of the biology of the genus is

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based mainly on one species, *P. viridans*, known from North and Central America, whose life cycle, foraging, and reproductive behavior has been described by several authors (Whitcomb 1962, Whitcomb *et al.* 1966, Randall 1977, 1982, Turner 1979, Fink 1986, 1987, Willey & Adler 1989, Arango *et al.* 2000). This species has been found associated with some plant species from various localities and, in at least two areas, it positively interacts with host plants by consuming phytophagous insects (Arango *et al.* 2000, Louda 1982). In fact, *P. viridans* was considered to be a good biological control agent in North American agroecosystems (Nyffeler *et al.* 1987; Nyffeler *et al.* 1992a, b).

In this study, we investigated the association of *Peucetia* with plants bearing glandular hairs over several regions of the world. These associations were either observed directly by us or compiled from the literature. To better understand this kind of spider–plant interaction, we particularly investigated the association of two common Neotropical species, *Peucetia rubrolineata* and *P. flava*, with plants with glandular trichomes in three localities in Southeastern Brazil, over a 20-yr period.

METHODS

STUDY SITES.—Associations between *Peucetia* species and plants with glandular trichomes were investigated in three localities in Southeastern Brazil. The first survey was done in the Horto Florestal, in Sumaré city (22°47′ S, 47°17′ W), São Paulo State. This area comprised 15 ha of *Eucalyptus* plantation with an understory of native shrubby species, especially species of the Solanaceae. Additional data were obtained in an area of 7 ha located about 30 km from Sumaré, close to the margins of a semi-deciduous forest, at Santa Elisa farm, Campinas city (22°56′ S, 47°03′ W). The climate of the region comprising these two areas consists of distinct dry/cold (May–September) and wet/warm (October–April) seasons, with mean annual rainfall and temperature of 1403 mm and 20.6°C, respectively (Mello *et al.* 1994). The third area was the Reserva Florestal da Companhia Vale do Rio Doce (CVRD; 19°26′ S, 40°03′ W), 30 km north from Linhares city, Espírito Santo state, a forest reserve covered mainly by Atlantic Forest vegetation. The reserve comprises 22,000 ha of forest with altitude varying from 28 to 65 m above sea level and a soil rich in sand. The weather is seasonal, with rainfall varying monthly from 30 mm in the dry season (around June) to 226 mm in the wet season (January). The mean annual rainfall is 1320 mm, and the temperature varies from 10°C to 30°C (Jesus 1988). Samplings were concentrated along a track of 40 km at the understory of a rain forest and in a 4 ha area of nativo vegetation (see Romero & Vasconcellos-Neto 2004a), a locally common vegetation type on sandy soil, dominated by cacti, bromeliads, herbs, and small shrubs (Jesus 1988, Peixoto & Gentry 1990)

LOCAL ASSOCIATION WITH PLANTS BEARING GLANDULAR TRICHOMES.—The two species investigated in this study, *P. rubrolineata* and *P. flava*, are the most common representatives of the genus in South America. Both species are widely distributed all over Brazil and occur sympatrically in several localities (Santos & Brescovit 2003). To verify whether these lynx spiders live strictly associated with plants bearing glandular hairs in a local scale, we compared their frequency on species of Solanaceae with and without glandular hairs, as well as between species of Solanaceae with glandular hairs and neighboring plants of several families without such type of hair. The family Solanaceae provides a suitable system to test for host plant selection by *Peucetia* spp., since it is very common and diverse in southeastern Brazil, and is relatively homogeneous regarding morphological traits (*e.g.,* aculeus, branch architecture, leaf size, and shape) that could influence its occupation by spiders, and presents congeners with and without glandular hairs.

Samplings were done monthly, between 0700 h and 1300 h, over 14 mo (8 April 1977 to 10 May 1978) selecting the first 10–50 plants (0.2–2.5 m tall) of each plant species found in an area of 15 ha in Sumaré. The varying number of plants sampled occurred because some species were abundant and others were rare (Vasconcellos-Neto 1980). Because the samples in Sumaré were done monthly, we probably sampled the same plant more than once. However, a time span of 1 mo is enough to avoid data dependence (*i.e.,* temporal pseudoreplication), since during this period a spider can potentially migrate to another plant, change instar, or the host plant can change in architecture (*i.e.,* size, number of branches, and leaves). Therefore, data for Sumaré are presented as a number of records of spiders and host plants, instead of number of individuals.

Each solanaceous plant found at Sumaré was inspected in total, including branches, leaves, and stems. The plants sampled were identified and the presence/absence of glandular hairs, types of hairs (simple, starred, glabrous, glandular), and density of glandular hairs were noted. The type and density of glandular trichomes for each plant species were recorded under a stereoscopic microscope from samples (5 × 5 mm) taken from the central part of the leaf ($N = 4$). The hair density of each sample was expressed as the sum of the number of hairs found both on the upper and the lower side of the leaves. In addition, we recorded the number of specimens of each species of *Peucetia* found over the plants. Additional data were obtained from the Santa Elisa farm in February 1996, by inspecting all solanaceous plants using the same procedures as in Sumaré.

The frequency of spiders found on solanaceous species bearing glandular hairs and neighboring nonsolanaceous plants were compared monthly in Sumaré, between April 1977 and May 1978, using *Solanum incarceratum*, the most common species bearing high density of glandular hairs in this area. For each *S. incarceratum* surveyed, we sampled 1–4 nearest nonsolanaceous plants (similar in size, ~1.0 m tall) without glandular hairs, in a radius of up to 1.5 m from the solanaceous plant. A similar procedure was followed to obtain additional data in Linhares, except that the solanaceous plants bearing glandular hairs (*S. cordifolium* and *S. thomasiifolium*) were sampled yearly, not monthly. The samplings of *S. cordifolium* and *S. thomasiifolium*, as well as their neighboring plants, were done in the rain forest understory and in the nativo vegetation, respectively, between 1989 and 1997. The same procedures used in Sumaré were followed in Linhares to select neighboring plants and to find spiders.

LARGE SCALE ASSOCIATION WITH PLANTS BEARING GLANDULAR TRICHOMES.—To verify whether spiders of the genus *Peucetia* are associated with plants with glandular hairs over a geographic scale, we compiled several records of plants occupied by *Peucetia* species, both from direct observations and from the literature. The field observations were made during several trips, covering a wide range of habitats in South and Central America, for the period 1974 to 2006. The information recorded includes the species found and the host plant they inhabited. For each host plant, we recorded its genus/species, presence/absence of glandular hairs, the habit (herbaceous, shrub or tree), and the vegetation type in the habitat. The types of vegetation from each geographic region were classified according to National Geographic Society (2001), IBGE (1993), and Davis *et al.* (1997). Areas of variable vegetation surrounded by a matrix of rain forest were classified as restinga, *i.e.*, communities on sandy soil close to the shore dominated by cacti, bromeliads, herbs, and small shrubs (Lacerda *et al.* 1984) and nativo vegetation, *i.e.*, similar to restinga, but far from the shore (Jesus 1988, Peixoto & Gentry 1990); grasslands were pastures and old fields areas surrounded by a matrix of araucaria forest and tropical dry forest, and rupestrian fields were open-rock pioneer vegetation (Menezes & Giulietti 1986, Davis *et al.* 1997).

The spiders collected were preserved in 70 percent ethanol for later identification, and voucher specimens were deposited in the arachnological collection of the Laboratório de Artrópodes, Instituto Butantan, in São Paulo. The botanical material was deposited in the herbarium of the Department of Botany, Universidade Estadual de Campinas.

Literature records were compiled from original taxonomic descriptions, taxonomic revisions, and publications on natural history of *Peucetia* species worldwide. In most cases, data from literature presented no or little information on the presence/absence of glandular hairs, or the plant type occupied by the spiders. In these cases, we obtained information through specialized botanical literature.

RESULTS

LOCAL ASSOCIATION WITH PLANTS BEARING GLANDULAR TRICHOMES.—We obtained 938 records of *P. rubrolineata* in 2864 records of 13 solanaceous species in Sumaré (Table 1). In this area, 56 percent and 46 percent of the individuals and species of the Solanaceae recorded, respectively, had glandular hairs. Most of the *P. rubrolineata* recorded (96.6%, $N = 906$) were from Solanaceae bearing glandular hairs (Table 1), with a difference statistically significant (*G*-test; $G = 802.5$, 1 df, $P < 0.001$). *Peucetia rubrolineata* was more frequently found on *S. incarceratum* (68.7%), followed by *S. sublentum* (11.6%), than other solanaceous plants (Table 1). The number of spiders recorded per plant species and the percentage of plants of each solanaceous species inhabited by the spiders were correlated with the mean density of glandular hairs of each plant species (Table 1; records: $R^2 = 0.33$, $F_{1,11} = 5.51$, $P = 0.039$; percentage: $R^2 = 0.69$, $F_{1,11} = 24.17$, $P < 0.001$).

In Campinas, ten species of Solanaceae (177 individuals) were sampled, but only 2.8 percent of them had glandular hair (Table 2). In contrast to our findings in Sumaré, only one individual of *P. rubrolineata* was found in Campinas, on a plant without glandular hairs.

In Sumaré, all the plants of *S. incarceratum* recorded ($N = 332$) were inhabited by *P. rubrolineata*, but none of the neighboring plants ($N = 1288$) had spiders (Table 3). In Linhares, from 1989 to 1994, 84 percent (133 of 158) of *S. cordifolium* were inhabited by *P. rubrolineata*, while only 1.1 percent (4 of 366) of the neighboring plants were occupied by this spider species. In this area, we also found *P. flava* on *S. thomasiifolium*. All individuals of this plant species ($N = 70$) were inhabited by *P. flava* in 1997, while none of its neighboring plants ($N = 80$) had spiders (Table 3). The mean density of spiders per individual of *S. incarceratum* (Sumaré), *S. cordifolium* (Linhares), and *S. thomasiifolium* (Linhares) was, respectively, 1.9, 9.0, and 12.9 (Table 3).

LARGE SCALE ASSOCIATION WITH PLANTS BEARING GLANDULAR TRICHOMES.—The lynx spider species *P. rubrolineata* and *P. flava* were associated with plants bearing glandular hairs over a wide geographic range throughout South America (Table S1). *Peucetia rubrolineata* were recorded from 22 shrubby plant species living in rain forests, nativo vegetation, and semideciduous forests in ten localities of four Brazilian states. Two of these host plants were exotic (*Jatropha podagrica* and *Plectranthus barbatus*; Table S1). Eighty percent of the host plants had glandular hairs. *Peucetia flava* occurred on 18 plant species living in semideciduous forests, rain forests, nativo vegetation, cerrado, grasslands from araucaria moist forests, rupestrian fields, and restingas in 13 localities of six Brazilian states. Almost all the host plant species were shrubby and had glandular hairs (Table S1). The most common plant families inhabited by *P. rubrolineata* and *P. flava* were members of the Solanaceae, Melastomataceae, and Asteraceae.

In Table S1, information on host plants of *Peucetia* spp. has been compiled from the literature. Of the 43 known species of *Peucetia*, data on host plants are only available for 13 species. Of these species, ten have been sampled from plants with glandular hairs living in an extensive variety of phytophysiognomies from several countries ranging from Colombia, Panama, Costa Rica, Mexico, USA (Florida and California), Yemen, Israel, Egypt, Namibia, South Africa, and Spain. We do not have enough information to say whether some species (*e.g., P. madagascariensis*, *P. pulchra*, and *P. striata*) were associated with plants bearing glandular hairs.

DISCUSSION

Our findings show that the lynx spiders *P. rubrolineata* and *P. flava* are strongly associated with plants bearing glandular hairs in a local

TABLE 1. *Records of* Peucetia rubrolineata *on several solanaceous species with absence of glandular trichomes or presence of these leaf structures in different densities, in Sumaré.*

Plant species	Trichome type[T]	Trichome location[L]	Dens.$^{\mathrm{Dad}}$ (mean ± SE)	Dens.$^{\mathrm{Dab}}$ (mean ± SE)	NS	%S	NP	%P
Cestrum sendtnerianum	–	–	–	–	0	0	681	0
Solanum variabile	S	–	–	–	0	0	192	0
S. paniculatum	S	–	–	–	0	0	226	0
S. mauritianum	S	–	–	–	0	0	176	0
S. robustum	S	–	–	–	30	3.2	210	5.7
S. affine	S	–	–	–	2	0.2	100	2
S. capsicoides	S	–	–	–	0	0	25	0
S. megalochiton	S,Gl	S	–	–	21	2.3	236	8.9
S. sisymbriifolium	S,Gl	S,L	11.0(3.3)	23.2 (4.5)	0	0	3	0
S. palinacanthum	S,Gl	S,L	43.7(26.2)	195.0 (76.1)	51	5.4	509	7.6
S. viarum	S,Gl	S,L	129.2(21.6)	457.5 (25.9)	81	8.6	131	26.7
S. incarceratum	S,Gl	S,L	207(10.1)	223.5 (43.7)	644	68.7	332	59.3
S. sublentum	S,Gl	S,L	267.5 (63.2)	166.2 (34.8)	109	11.6	43	58.1

[T] S = starred, Gl = glandular.

[L] location of glandular trichomes in the plant: S = stem, L = leaf.

"Dad" and "Dab" are density of glandular trichomes (number/25 mm^2) on the adaxial and abaxial side of the leaves, respectively; NS = number of spiders recorded; %S = percentage of spiders on each plant species; NP = number of plants recorded; %P = percentage of plants of each solanaceous species inhabited by the spiders.

scale. Our observations also suggest that both species can use sticky plants, both immatures and adults as well as females with egg sacs. The reason why *Peucetia* species have specialized to these plants may be the function of the glandular hairs as insect traps, which facilitate prey capture by trapping or preventing insects to dislodge and escape (Dolling & Palmer 1991, Ellis & Midgley 1996, Romero & Vasconcellos-Neto 2004b). On several occasions during the study, we observed *Peucetia* preying on insects adhered on the glandular hairs.

The spiders *P. rubrolineata* and *P. flava* were common in regions with a dense cover of plants bearing glandular hairs (*e.g.,* Sumaré), but relatively rare in regions (*e.g.,* Campinas) where these plant traits were rare or absent. Moreover, in the period of 1974–1976 more than 100 plants of *Lantana camara* (Verbenaceae) were inspected in Sumaré, and in other regions of Campinas, but no *Peucetia* species was found upon them. In these regions, *L. camara* do not bear glandular trichomes (J. Vasconcellos-Neto, pers. obs.). In contrast, this plant species has glandular trichomes in the shoots and immature leaves in Linhares and Porto Seguro (Bahia state), and nine individuals of *P. rubrolineata* and 17 of *P. flava* were observed on them (Table S1). These results suggest that the spatial distribution of these *Peucetia* spp. may be limited by the availability of host plants having glandular hairs. The lynx spiders *P. rubrolineata* and *P. flava* are associated with plants bearing glandular hairs over a wide geographic scale, reinforcing the conclusion that these species strongly prefer this type of plant as foraging microhabitat.

TABLE 2. *Solanaceous species surveyed on the Santa Elisa farm. These species did not present glandular trichomes, except* Physalis angulata.

Plant species	Trichome type[T]	NS	NP
Cestrum laevigatum	Si	0	7
Solanum paniculatum	S	0	5
S. mauritianum	S	0	34
S. conccinum	S, Si	0	65
S. oocarpum	S	1	11
S. americanum	Si	0	31
S. affine	Si	0	17
S. alteernatopinatum	Si	0	1
S. capsicoides	S	0	1
*Physalis angulata**	G	0	5

[T] Si = simple, S = starred, Gl = glandular.

NS = number of spiders surveyed, NP = number of plants surveyed.

*Glandular trichomes present on the stems, but absent on the leaves.

Another eight *Peucetia* species were also found associated with plants bearing this type of trichome, in several regions in the world. For instance, we have found *P. longipalpis* occurring on three plant species bearing glandular hairs in Colombia and Panama. *Peucetia viridans* was associated with five plant species bearing glandular hairs in Panama, Mexico, and U.S.A. (Florida and California). Lawrence (1964) reported that *P. maculifera* is found mainly on *Helichrysum cooperi*, a common South African plant with very sticky leaves on which thousands of insects are trapped. From South Africa, *P. nicolae* and *P. transvaalica* were twice collected from plants with glandular hairs. *Peucetia viridis*, which occurs widely throughout Africa and the Mediterranean Region, was recently collected from Bushman's Grass (*Schmidtia kalahariensis*) in the Kalahari (Dippenaar-Schoeman 2005). This annual grass is available for only a short period after good rains. It has an unpleasant smell and is covered with glands that produce an acidic substance. Over a period of a week of intensive collecting, *P. viridis* was the only spider species present on this grass. *Peucetia viridis* was also reported by Simon (1890) to

TABLE 3. *Records of* Peucetia rubrolineata *and* P. flava *on three* Solanum *species (*S. incarceratum*,* S. cordifolium*, and* S. thomasiifolium*) bearing glandular trichomes and on their neighboring plants without glandular trichomes, at Sumaré (SP) and Linhares (ES), during different years.* N *= total number of records.*

	Solanum species			Neighboring plants		
Year	Inhabited	Uninhabited	*N*	Inhabited	Uninhabited	*N*
P. rubrolineata on *S. incarceratum* (Sumaré)						
1977–1978	332	0	644	0	1288	0
P. rubrolineata on *S. cordifolium* (Linhares)						
1989	56	14	489	0	94	0
1990	20	2	175	0	96	0
1993	25	4	256	2	136	2
1994	32	5	275	2	36	2
Total	133	25	1195	4	362	4
P. flava on *S. thomasiifolium* (Linhares)						
1997	70	0	900	0	80	0

occur exclusively on *Ononis hispanica*, a Spanish plant with glandular hairs. This was confirmed by Barrientos (1991) who, based on the geographic distribution of these species in Spain, speculated that the association of *P. viridis* with *O. hispanica* might be host plant specific. However, in southern Africa, *P. viridis* commonly occurs on several plant species without glandular hairs, including acacia trees (*e.g., Acacia haematoxylon*, *A. nigrescens*), crops (pistachio), or grasses. These observations suggest that the availability of plants with glandular hairs does not impose limits on the distribution of this species, although a preference for such plants may occur in some localities (A. Dippenaar-Schoeman, pers. obs.). *Peucetia arabica* was observed by Simon (1890) in southern Yemen and Egypt to occur frequently on plants bearing glandular hairs (*e.g., Cleome trinervia* and *C. droserifolia*), but rarely on plants without this type of structure. This was supported by Levy (1999) who found *P. arabica* on *Cleome* plants bearing glandular hairs in southern Israel. There is evidence that *Peucetia crucifera* is also associated with plants with glandular hairs (see Table S1). Although these observations do not present reliable evidence of preference for plants with glandular trichomes, they suggest that this type of association is relatively common even if in several instances *Peucetia* species were also recorded in plants without glandular hairs (Tables 1 and S1).

In conclusion, *P. rubrolineata* and *P. flava* seems to be preferentially associated with plants bearing glandular hairs in different vegetation types (phytophysiognomy) in Brazil. These data are supported by observation on eight other species of this genus that were also associated with plants having this type of trichome in several regions in the world. We suggest that the association of *Peucetia* species with plants bearing glandular trichomes may have evolved because sticky structures may facilitate prey capture by the spiders. Future collections in other parts of the world, if implemented with an adequate sampling protocol, could be extremely useful to determine how widespread is this habitat preference. It would be particularly important to investigate possible variations in the degree of specialization of different species for plants with glandular hairs. Given the fact that some records show *Peucetia* species using plants without this trait, studies on how species select plants as foraging sites in areas with low availability of optimal plants may be a promising area for future research. In addition, the possible beneficial effects of these spiders for their host plants remain open for future investigations.

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