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Relação de custo/benefício na interação entre a aranha *Peucetia flava* (Oxyopidae) e a planta *Rhynchanthera dichotoma* (Melastomataceae)

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2009

José Cesar de Moraes Filho

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Dissertação apresentada para obtenção do título de Mestre em Ciências Biológicas, área de Ecologia junto ao Programa de Pós-Graduação em Biologia Animal do Instituto de Biociências, Letras e Ciências Exatas da Universidade Estadual Paulista “Júlio de Mesquita Filho”, Campus de São José do Rio Preto.

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**Dedico este trabalho aos
meus pais, à Kátia e
ao meu filho Nand**

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RESUMO

Até dez espécies de aranhas do gênero *Peucetia* (Oxyopidae), incluindo duas espécies sul-americanas, *P. flava* e *P. rubrolineata*, vivem associadas a várias espécies de plantas com tricomas glandulares nas regiões Neotropical, Paleártica, Neártica e Afrotropical; estas associações provavelmente evoluíram porque insetos aderidos aos tricomas glandulares podem ser utilizados como fonte de alimento pelas aranhas. Na região noroeste do estado de São Paulo, indivíduos de *P. flava* ocorrem estritamente sobre a planta com tricomas glandulares *Rhynchanthera dichotoma* (Melastomataceae). Neste sistema nós desenvolvemos experimentos para testar quais os custos e benefícios de *P. flava* para *R. dichotoma* e se há condicionalidade nestas associações. Além disso, testamos o papel dos tricomas glandulares como mediadores destas associações aranhas-plantas. Nós observamos que estas aranhas atuam como guarda-costas das plantas e que este efeito é temporalmente condicional; forças base-topo minimizam os efeitos das aranhas durante o período chuvoso. Além disso, estas aranhas indiretamente aumentaram a aptidão da planta pela redução do número de botões inviáveis. Os tricomas glandulares podem ter uma função análoga ao de uma teia pela retenção de presas. As aranhas preferem plantas com tricomas glandulares intactos e permanecem mais tempo sobre estas do que em plantas com tricomas glandulares removidos. Análises isotópicas de ^{15}N mostraram que estas aranhas podem se alimentar tanto de insetos vivos como de carcaças de insetos aderidos aos tricomas glandulares, exibindo hábitos carniceiros. Estes resultados demonstram que esta associação é um mutualismo facultativo.

ABSTRACT

Up to ten species of the genus *Peucetia* (Oxyopidae), including two South American species, *P. flava* and *P. rubrolineata*, live strictly associated with many species of glandular plants in Neotropical, Palearctic, Afrotropical and Nearctic regions; this associations probably evolved because insects adhered to these sticky structures may be used as prey by the spiders. In southeastern Brazil specimens of *P. flava* were reported to occur strictly on *Rhynchanthera dichotoma* (Melastomataceae), a glandular shrubby plant that typically inhabits swamps. In this system we used experiments to test the cost and benefit of these spiders to plants and also the role of glandular trichomes as mediators of this association. We found that these spiders act as plant body-guards and this function is temporally conditional; bottom-up forces mitigate the impact of spiders during the rainy season. Moreover, these spiders indirectly increase fitness of the host plant by reducing the number of unviable flower buds, without influence on the seed set. Glandular trichomes probably have an analogous function of a web by capture or prey retention. Spiders prefer plants with intact glandular trichomes, remaining much longer on these ones than on those with these structures removed. Isotopic analyses of ^{15}N demonstrated that these spiders fed on live and dead prey adhered to glandular trichomes, exhibiting a scavenging behavior. These results demonstrate that this association is a facultative mutualism.

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1. INTRODUÇÃO

Mutualismo

Mutualismo é uma interação que resulta em benefícios recíprocos, tanto para o indivíduo como para a população, entre duas ou mais espécies (Boucher et al. 1982). Esta rede de benefícios recíprocos pode surgir a partir de diferentes fatores que definem o tipo de interação mutualística, tais como o grau de associação entre duas espécies, o grau da interação que é necessária para a sobrevivência de cada espécie (i.e., obrigatório ou facultativo) (Heil & McKey 2003), os tipos de benefícios (e.g., proteção, dispersão, polinização) (Herrera & Pellmyr 2002), o grau de especialização recíproca (coevoluídos ou não coevoluídos) (Thompson & Cunningham 2002), os padrões temporais e espaciais das associações (Billick & Tonkel 2003) e a forma pela qual é transmitido o benefício (direto ou indireto) (Boucher et al. 1982; Addicott 1984; Bronstein 1994a).

Uma interação deve ser vista como mutualística apenas se a aptidão e/ou o crescimento populacional dos parceiros diminuïrem na ausência da interação (Boucher et al. 1982). No entanto, os mecanismos que promovem persistência e colapso dos mutualismos podem variar no espaço e no tempo e, quando considerados do ponto de vista da relação de custo/benefício, torna-se evidente que as respostas de uma interação são extremamente dinâmicas (Bronstein 1994b). Os indivíduos variam em suas expressões fenotípicas, populações variam em sua estrutura e, como consequência, as interações variam em suas respostas (Thompson 1988). Essas respostas, quando dependentes dos fatores bióticos e abióticos que variam no tempo e espaço, são denominadas respostas condicionais (Thompson 1988, 1999; Cushman & Whitham 1989; Bronstein 1994b; Thompson & Cunningham 2002). Algumas interações podem variar desde parasitismo para mutualismo (Thompson 1988; Cushman & Whitham 1989; Thompson & Pellmyr 1992; Thompson & Cunningham 2002; Thomson 2003). Por exemplo, a interação entre *Lithophragma parviflorum*, uma planta herbácea, e a mariposa *Greya politella*, um polinizador e parasita floral, pode ser fortemente mutualística em determinado habitat, mas comensalista ou mesmo parasítica em habitats vizinhos (e.g., Thompson & Cunningham 2002).

Os principais exemplos de mutualismo entre animais e plantas são representados por interações entre fanerógamas e polinizadores ou dispersores de sementes (Faegry & van der Pijl 1979; Jordano 2000), entre formigas e plantas com nectários extraflorais ou mirmecófitas (Janzen 1966), entre ácaros e plantas com domáceas (revisado em Romero & Benson 2005), figueiras e vespas do figo (Bronstein & Hossaert-McKey 1995; Kjellberg et al. 2001; Cook & Rasplus 2003) e yucca e a mariposa da yucca (Addicott 1998; Pellmyr & Huth 1994; Pellmyr

et al. 1996). Embora grande número de interações positivas conhecidas seja de casos de mutualismos (Stachowicz 2001), poucos estudos demonstram um aumento na aptidão ou taxa de crescimento de ambas as espécies presentes em uma interação (Boucher et al. 1982). Tipicamente, a maioria dos estudos analisa os benefícios do ponto de vista de apenas uma das espécies na interação. Em interações animais-plantas, por exemplo, as plantas são freqüentemente mais estudadas que seus parceiros animais (Bronstein 1994a).

Muitas famílias de aranhas habitam vegetação e podem potencialmente afetar direta e indiretamente a abundância e estrutura de comunidades de artrópodes e os níveis de herbivoria (Riechert & Bishop 1990; Spiller & Schoener 1990, 1994; Carter & Rypstra 1995; Polis & Hurd 1995; Schmitz 1998; Schmitz *et al* 2000; Schmitz & Suttle 2001; Halaj & Wise 2001) e muitos estudos demonstram algum tipo de relação benéfica entre aranhas e plantas (Louda 1982; Ruhren & Handel 1999; Whitney 2004; Romero & Vasconcellos-Neto 2004b; Romero et al. 2006; Romero et al. 2008). Porém, pouco é conhecido sobre interações mutualísticas em sistemas aranhas-plantas (e.g., Whitney 2004; Romero et al. 2008).

Associações específicas entre aranhas e plantas

Estudos recentes têm reportado associações específicas entre aranhas e determinadas estruturas vegetais (Figueira & Vasconcellos-Neto 1991, 1993; Arango et al. 2000; Rossa-Feres et al. 2000; Romero & Vasconcellos-Neto 2003, 2004a, b, c, 2005a, b, c; Dias & Brescovit 2004; Romero et al. 2008). Até o momento, os exemplos mais estudados de estruturas vegetais que mediam interações aranha-planta são folhas dispostas em forma de roseta (e.g., Bromeliaceae), tricomas glandulares e nectários extraflorais (Romero & Vasconcellos-Neto 2007).

Nove espécies de aranhas da família Salticidae vivem associadas à Bromeliaceae em diversas fisionomias vegetais do Brasil, Paraguai, Bolívia e Argentina (Romero 2006). Dessas, a aranha bromelícola mais bem estudada é *Psecas chapoda*, que ocorre estritamente associada à *Bromelia balansae*. Esta bromélia apresenta folhas finas e longas repletas de espinhos, as quais se dispõem em uma arquitetura de roseta que não acumula água. *P. chapoda* reconhece a arquitetura e morfologia destas folhas e seleciona tais plantas (Omena & Romero 2008), as quais provêem abrigo e sítios de forrageamento e reprodução, além de berçário para os imaturos (Rossa-Feres et al. 2000; Romero & Vasconcellos-Neto 2005a, b).

Além disso, *P. chapoda* contribui com a nutrição e taxa de crescimento de suas plantas hospedeiras (Romero et al. 2006).

Dez espécies de aranhas do gênero *Peucetia* (Oxyopidae) ocorrem associadas a várias espécies de plantas com tricomas glandulares (e.g., Solanaceae, Asteraceae, Melastomataceae) em diversos tipos de vegetação em mais de 36 localidades nas regiões Neotropical, Paleártica, Neártica e Afrotropical (Vasconcellos-Neto et al. 2007). Este trabalho reporta que dentre estas espécies de *Peucetia*, as sul-americanas *P. flava* e *P. rubrolineata* são fortemente associadas a plantas glandulares em diversas regiões geográficas, onde estas plantas ocorrem em grande abundância. A preferência de *P. flava* e *P. rubrolineata* por plantas com tricomas glandulares ocorre em diversas regiões geográficas da América do Sul.

Tricomas glandulares são estruturas adesivas que evoluíram como uma defesa contra herbívoros (Levin 1973), entretanto, podem atuar como uma armadilha de insetos, o que facilita a captura de presas pelo aprisionamento ou dificuldade de locomoção (Dolling & Palmer 1991; Ellis & Midgley 1996; Romero & Vasconcellos-Neto 2004a). Esta especialização de aranhas *Peucetia* por plantas com tricomas glandulares pode ter evoluído porque insetos aderidos a estas estruturas adesivas podem ser usados pelas aranhas como itens alimentares (Romero & Vasconcellos-Neto 2004a; Vasconcellos-Neto et al. 2007; Romero et al. 2008). Entretanto, pouco se sabe sobre a evolução de tal especialização, quais os benefícios da presença dessas aranhas para suas plantas hospedeiras, bem como o papel dos tricomas glandulares para as aranhas (Romero et al. 2008).

Dos parasitismos aos mutualismos em relações aranhas–plantas

A presença de aranhas pode exercer efeitos significativos na redução dos níveis de herbivoria foliar e floral (Romero & Vasconcellos-Neto 2004b; Romero et al. 2008) sendo benéfica, portanto, a sua presença para a planta hospedeira. Por outro lado, uma vez sobre flores, podem interferir nas relações mutualísticas das plantas com polinizadores e decrescer a aptidão da sua planta hospedeira (Gonçalves-Souza et al. 2008). E, além disso, aranhas também podem receber benefícios por ocorrerem associadas a plantas (Romero et al. 2008). Analisando as relações de custo/benefício em associações aranhas–plantas, podemos concluir que a presença de aranhas em plantas hospedeiras pode variar de parasitismo a mutualismo, apresentando também respostas intermediárias ou neutras em que custos e benefícios se igualam. Abaixo descrevo esta variação com exemplos de alguns sistemas aranhas–plantas.

Aranhas da família Thomisidae ocorrem mais frequentemente sobre flores e alguns estudos reportam que algumas destas aranhas (e.g., *Misumena vatia*) não ocorrem aleatoriamente sobre tais estruturas, pois reconhecem aquelas que atraem maior quantidade de presas (Morse & Fritz 1982; Chien & Morse 1998), ou seja, exploram as mesmas características florais preferidas por polinizadores, como quantidade de néctar, cores e odores florais (e.g., *Thomisus spectabilis*) (Heiling & Herberstein 2004b; Heiling et al. 2004; Heiling et al. 2005). Heiling & Herberstein (2004a) demonstraram que as abelhas australianas *Austroplebia australis*, que co-evoluíram com a presença do predador *Thomisus spectabilis*, reconhecem sua presença sobre flores e as evitam, enquanto que as abelhas européias *Apis mellifera* introduzidas naquele continente, são mais atacadas por este predador.

De fato, predadores em flores interferem nas relações mutualísticas entre plantas e polinizadores e indiretamente decrescem a aptidão de sua planta hospedeira (Dukas 2001, 2005; Dukas & Morse 2003, 2005; Gonçalves-Souza et al. 2008). Por exemplo, Dukas & Morse (2003, 2005) reportam que a presença da aranha *Misumena vatia* em flores de *Asclepias syriaca* (Asclepiadaceae) reduziu o número de visitas de abelhas *Bombus ternarius* e *Apis mellifera* em mais de 50%, enquanto que não observaram efeitos significativos da presença de aranhas sobre a aptidão da planta. Já em um estudo recente, Gonçalves-Souza et al. (2008) demonstraram que a presença de modelos artificiais de tomisídeos sobre flores de *Rubus rosifolius* (Rosaceae) reduziu grandemente a taxa de visitação floral. Além disso, a presença desses modelos de aranhas reduziu o número de sementes em 42% e a biomassa dos frutos em 50%. Estes estudos demonstram uma relação potencialmente parasítica de aranhas para plantas.

A relação entre a aranha *Peuceitia viridans* e a planta *Haplopappus venetus* (Asteraceae) é um exemplo de interação em que a presença de aranhas exerce efeitos positivos e negativos dentro do sistema (Louda 1982) e estas respostas podem ser nulas se comparados os custos e benefícios. Neste sistema, o ataque de *P. viridans* aos visitantes florais reduziu em 17% a produção de sementes por ramo. Entretanto, o ataque aos herbívoros florais aumentou em 18% o número de sementes viáveis; o saldo entre custo e benefício da aranha para a planta é quase nulo. Entretanto, Ruhren & Handel (1999) demonstram que na interação entre *Chamaecrista nictitans* (Caesalpineaceae) e aranhas Salticidae, a presença destas é somente benéfica para a planta. Estas aranhas aumentam a produção de sementes em 8% e são atraídas para esta planta devido à presença de nectários extraflorais, que aumentam a chance de encontro de presas, as quais também são atraídas por tais estruturas, e podem ser usados como fonte de alimento pelas aranhas.

Os exemplos de mutualismos facultativos reportados em sistemas aranhas–plantas representam associações mediadas por nectários extraflorais (Whitney 2004), arquiteturas em roseta (Romero et al. 2006) e tricomas glandulares (Romero et al. 2008). Um dos primeiros casos de benefício recíproco reportado em sistemas aranhas–plantas é o da relação entre as aranhas sub-sociais *Phryganoporus candidus* (Desidae) e a planta com nectários extraflorais *Acacia ligulata* (Fabaceae) (Whitney 2004). Neste sistema mutualístico, a presença destas aranhas aumenta em até 6% a produção de sementes, enquanto que a presença de nectários extraflorais pode contribuir para a nutrição das aranhas. Ambos se beneficiam nesta relação. No entanto, Whitney (2004) não testa os custos da presença destas aranhas para as plantas. Um exemplo de associação mutualística mediada por arquitetura em roseta é observado na associação entre *P. chapoda* e *B. balansae*, em que as fezes das aranhas contribuem para a nutrição das bromélias e a arquitetura em roseta fornece abrigo e sítios de forrageamento e reprodução para as aranhas (Romero et al. 2006). Os exemplos de associações mutualísticas mediadas por tricomas glandulares são representados por associações entre aranhas *P. flava* e *P. rubrolineata* e a planta com tricomas glandulares *Trichogoniopsis adenantha* (Asteraceae) (Romero et al. 2008). Romero et al. (2008) demonstra que a presença de *P. flava* e *P. rubrolineata* em *T. adenantha* reduz os níveis de herbivoria foliar e floral, aumentando a aptidão da planta mesmo com uma redução marginal na proporção de ovários fertilizados. Em contrapartida, as aranhas que ocorrem nestas plantas apresentaram menor perda de biomassa, pois atuaram como carniceiras por até 20h, se alimentando de carcaças presas aos tricomas glandulares de *T. adenantha*. Em um estudo ainda mais recente, Morais-Filho & Romero (dados não publicados) demonstram uma interação somente benéfica entre *P. flava* e *R. dichotoma*. Contudo, neste sistema não há custos para a planta hospedeira em manter estas aranhas.

O sistema de estudo: uma síntese sobre a interação *Peucetia*–*Rhynchanthera*

Embora inúmeros estudos tenham reportado associações específicas entre aranhas e plantas, poucos descrevem a história natural destes sistemas, incluindo uso de microhabitat, fenologias, itens alimentares, bem como interações de aranhas e plantas com organismos de outros níveis tróficos em regiões Neotropicais (Arango et al. 2000; Romero & Vasconcellos-Neto 2003, 2005a, b, c). Vários indivíduos da aranha *Peucetia flava* ocorrem associados à planta com tricomas glandulares *Rhynchanthera dichotoma* na região noroeste do estado de

São Paulo. Durante 13 meses, de dezembro de 2005 a dezembro de 2006, nós monitoramos estes indivíduos e descrevemos sua história natural e uso de microhabitat. Os trabalhos resultantes deste estudo, integrantes de minha Monografia, seguem em anexo (vide anexos A e B). Abaixo descrevo sucintamente os principais aspectos deste sistema aranha-planta.

A planta *R. dichotoma* é um arbusto (0,5-2,0 m altura) com tricomas glandulares que ocorre em brejos e ecossistemas aquáticos temporários na região de São José do Rio Preto. Esta planta é frequentemente habitada por artrópodes de diversas guildas, incluindo fitófagos (Curculionidae, Miridae, Aphididae, cigarrinhas etc.) e predadores (aranhas, Reduviidae). Também, diversos insetos são eventualmente aderidos aos tricomas glandulares (e.g., formigas, Chironomidae, Aphididae etc.), que são bastante densos nas folhas e caules jovens desta espécie de planta. A aranha *P. flava* é um predador errante, que não constrói teia, comum sobre esta planta. Suas presas incluem fitófagos, polinizadores, outros predadores e artrópodes aderidos aos tricomas glandulares.

Apesar da grande diversidade de plantas encontradas na área de estudo (e.g., Asteraceae, Melastomataceae, Poaceae, Zingiberaceae), *P. flava* foi observada somente em *R. dichotoma*, onde freqüentemente exibia comportamentos de forrageio e reprodução; foram observadas ootecas durante quase todos os meses de estudo. Isto sugere que em nosso local de estudo esta espécie de aranha ocorre estritamente associada a esta planta com tricomas glandulares. Nas regiões nordeste, sudeste e sul do Brasil *P. flava* ainda é encontrada em outros 16 arbustos com tricomas glandulares, o que reforça a hipótese de uma alta fidelidade destas aranhas com tricomas glandulares (Vasconcellos-Neto et al. 2007). Esta especialização possivelmente se deve a função análoga dos tricomas glandulares a uma teia, o que facilita a captura de presas pelo aprisionamento ou dificuldade de locomoção sobre os mesmos. Em campo, observamos indivíduos de *P. flava* se alimentando de insetos aderidos aos tricomas glandulares (e.g., formigas, Chironomidae, Aphididae) e Romero et al. (2008) demonstraram que esta aranha se alimenta até de carcaças presas aos tricomas glandulares de *Trichogoniopsis adenantha*.

Análises de regressão múltipla demonstraram que ao longo do ano a distribuição da população de *P. flava* sobre *R. dichotoma* esteve correlacionada a diferentes fatores, como altura da planta, número de artrópodes e número de folhas. Análises similares também demonstraram que o aumento do tamanho populacional de *P. flava* é fortemente influenciado pelo aumento na abundância de folhas e de artrópodes aderidos aos tricomas glandulares. Isso sugere que plantas com maior número de folhas representam melhores sítios de forrageamento e proteção (e.g., Gunnarsson 1990; Romero & Vasconcellos-Neto 2005b), pois

apresentam maior probabilidade de insetos ficarem aderidos aos tricomas glandulares. Estes resultados demonstram que tricomas glandulares, além de intermediarem associações aranha-planta (Vasconcellos-Neto et al. 2007), podem também influenciar a distribuição e a flutuação sazonal de aranhas.

O tamanho populacional de *P. flava* oscilou pouco ao longo do ano. Os eventos de acasalamento, produção de ootecas, dispersão e crescimento dos jovens ocorreram ao longo de todo o ano, independentemente da sazonalidade de fatores abióticos (chuva e temperatura). Esta estabilidade incomum observada na flutuação populacional de *P. flava* pôde ser explicada pela proximidade de *R. dichotoma* a um curso d'água. A proximidade com a água pode ter provido esta população com recursos alóctones: insetos aquáticos (e.g., Chironomidae) migram para o meio terrestre e ficam aderidos aos tricomas glandulares, mantendo a quantidade de recursos alimentares mesmo nos períodos de seca, o que mantém a população de *P. flava* estável.

A associação *Peucetia* – *Rhynchanthera* representa um sistema favorável para testar relações de custo/benefício em sistemas aranhas–plantas, bem como investigar o papel dos tricomas glandulares como mediadores de mutualismo entre estes organismos. Logo, as principais questões abordadas neste estudo foram: (1) *P. flava* altera a abundância de artrópodes e as taxas de herbivoria em *R. dichotoma*? (2) Este efeito é consistente temporalmente? (3) A aranha decresce ou aumenta a aptidão da planta? (4) A aranha recebe benefícios por ocorrer nos tricomas glandulares de *R. dichotoma*?

Figura 1. (A) Fêmea adulta de *Peucetia flava* sobre *Rhynchanthera dichotoma*; (B) *R. dichotoma*; (C) Miridae sp. andando sobre tricomas glandulares de *R. dichotoma*; (D) Macho adulto de *P. flava*; (E) Curculionidae sp.; (F) Pulgão preso nos tricomas glandulares de *R. dichotoma*; (G) Fêmea adulta aparentemente exibindo cuidado maternal; (H) Ramos reprodutivos de *R. dichotoma*; (I) Detalhe dos frutos de *R. dichotoma*; (J) Lepidoptera sp. sobre flor de *R. dichotoma*; (K) danos foliares em *R. dichotoma*; (L) Canibalismo em *P. flava*. Créditos de Gustavo Quevedo Romero e José Cesar de Morais Filho.

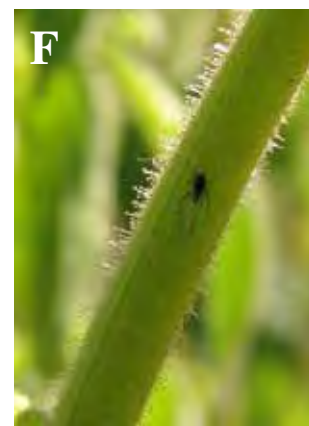
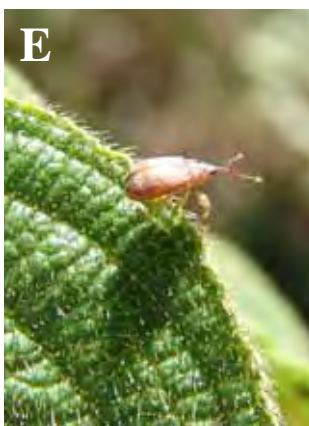


Figura 1.

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2. RELAÇÃO DE CUSTO/BENEFÍCIO

Morais-Filho, J.C. & Romero, G.Q. 2009. Plant glandular trichomes mediate protective mutualism in a spider-plant system (submetido).

Plant glandular trichomes mediate protective mutualism in a spider-plant system

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Running head: **glandular hairs and spider-plant mutualism**

Summary

1. Although several species of *Peucetia* (Oxyopidae) live strictly associated to plants bearing glandular trichomes worldwide, to date little is known whether these associations are mutualistic, i.e., if spiders improve plant fitness by protecting plants against natural enemies, and if glandular hairs provide benefits to the spiders (e.g., by improving prey capture). However, once upon flowers spiders can disrupt plant-pollinator mutualisms.
2. In this study we manipulated the presence of *Peucetia flava* on the glandular plant *Rhynchanthera dichotoma* (Melastomataceae) in the field, in the rainy and post-rain season, to test strength of its effects on plant fitness. In addition, we run independent field experiments to verify if these sticky structures improve spider fidelity to plants, if they improve prey capture by spiders, and if spiders can use both live and dead prey adhered.
3. *Peucetia* suppressed some species of foliar phytophages, but did not others. Albeit spiders have reduced levels of leaf herbivory, this phenomenon was temporally conditional, i.e., occurred only in the post-rain but not in the rainy season. Floral herbivory was also reduced in the presence of spiders, but these predators did not reduce individual plant fitness (seed set).
4. Plants with glandular trichomes removed retained fewer insects than those with such intact structures. Spiders remained longer on plants with glandular trichomes than on plants in which these structures were removed. Isotopic analyses (^{15}N) showed that spiders feed on live and dead labeled flies adhered to the glandular hairs in similar proportions.
5. Spiders provided no costs to the plants, however, increased indirectly plant fitness by reducing damages on flowers and flower buds. Temporal conditionality likely occurred because in the rainy season plant productivity exceeded herbivore consumption, thus dampening top-down effects. Glandular trichomes may function analogously to webs by increasing efficiency of prey capture with reduced costs in handling prey. In addition, specialization to live on glandular plants may have favored scavenging behavior in *Peucetia*, possibly an adaptation to periods of food scarcity. Once *Peucetia* is world-widely associated to glandular plants, mutualism involving spiders as plant bodyguards may be more common than previous thought.

Key-words: conditional outcomes, food web, glandular trichomes, host fidelity, Melastomataceae, Neotropical region, *Peucetia*, protective mutualism, spider-plant interaction, swamp, top-down and bottom-up forces.

Introduction

Mutualisms are interspecific interactions that benefit both partners maximizing their net fitness (Bronstein 1994a). Mutualisms are ubiquitous in nature (Janzen 1985) and play a central role in all ecosystems (Boucher, James & Keeler 1982; Thompson 1994; Bronstein 2001a; Stachowicz 2001). Every organism on earth is likely associated to one or more mutualistic partners (Bronstein, Alarcón & Geber 2006). Mutualism can be best viewed as a reciprocal exploitation between partners (Janzen 1985; Bronstein 2001b; Yu 2001). As a consequence, conflicts of interest arise between partners and, if considered in terms of cost/benefit, the responses of these associations are highly dynamics (Bronstein 1994b). For instance, the direction (i.e., antagonism to mutualism) and strength of these responses, as well as the mechanisms that promote persistence and collapse of mutualisms, can vary in space and time (Thompson 1999; Cushman & Whitham 1989; Bronstein 1994b; Thompson & Cunningham 2002; Billick & Tonkel 2003), a phenomenon called conditional outcome.

The main examples of mutualism between animals and plants are represented by interactions between phanerogamic and pollinators or seed dispersers, as well as ants and mites acting as plant bodyguards (Herrera & Pellmyr 2002). However, in animal-plant interactions, most studies examine the benefits from the viewpoint of only one species of the interaction; plants are often more studied than their animal partners (Bronstein 1994a). Spiders are very diverse and abundant predators on vegetation (Wise 1993; Foelix 1996), and can suppress herbivores, thus are considered as good biological control agents (Riechert & Lockley 1984). Moreover, they are influenced by variations in physical and architectural plant traits (Langellotto & Denno 2004; Romero & Vasconcellos-Neto 2005a). In addition, some spiders may even feed on plants, consuming pollen or nectar (e.g., Vogelei & Greissl 1989), while others maintain specific associations with plant species (e.g., Romero & Vasconcellos-Neto 2005a; Romero 2006; Vasconcellos-Neto, Romero, Santos & Dippenaar-Schoeman 2007). Despite these independent studies have shown that spiders can interact with plants in diverse ways, and that some of these associations are predictable over space and time, to date little is known about mutualistic interactions in spider-plant systems (Whitney 2004; Romero, Mazzafera, Vasconcellos-Neto & Trivelin 2006; Romero, Souza & Vasconcellos-Neto 2008). This may be explained because most of the studies that have shown some benefit in spider-plant interactions (e.g., Louda 1982; Ruhren & Handel 1999; Romero & Vasconcellos-Neto 2004) analyzed only part of the systems. The scarcity of studies on spider-plant mutualisms can also be explained by the widespread diet of spiders, which prey on both pollinators and

herbivores, as well as other predators (i.e., intra-guild predation), thus reducing their efficiency as mutualists on plants (Whitney 2004).

For the mutualisms between spiders and plants to occur and evolve, spiders need to be spatiotemporally and closely associated to a particular plant species or at least to a plant type (Romero *et al.* 2008). Currently, the most studied examples of plant structures that strengthen the fidelity of spiders and mediate these spider-plant interactions are leaves arranged in a rosette shape (e.g., Bromeliaceae) (Romero & Vasconcellos-Neto 2005a, b, c; Romero 2006; Romero *et al.* 2006) and presence of glandular trichomes (Vasconcellos-Neto *et al.* 2007; Romero *et al.* 2008). Romero & Vasconcellos-Neto (2005a, b, c) showed that the architecture of *Bromelia balansae* provides shelter against predators and fire, foraging and reproductive sites, as well as nurseries for *Psecas chapoda*. Moreover, Romero *et al.* (2008) demonstrated that spiders *Peucetia rubrolineata* and *P. flava* recognized and selected plants bearing glandular hairs; these sticky structures frequently trap and sometimes kill arthropods (Sugiura & Yamazaki 2006) that can be used by the spiders.

Up to 10 spider species of the genus *Peucetia* (Oxyopidae) live associated to many plant species bearing glandular trichomes in various vegetation types in Neotropical, Palearctic, Afrotropical and Nearctic regions (Vasconcellos-Neto *et al.* 2007). However, to date little is known why and how some members of *Peucetia* have evolved on glandular trichomes. In addition, little is known whether these associations are mutualistic, i.e., if spiders improve plant fitness by protecting plants against natural enemies, and if glandular hairs provide benefits to the spiders (Romero *et al.* 2008). On the other hand, once upon flowers spiders can disrupt plant-pollinator mutualisms. To better understand these contrasting interactions between *Peucetia* spiders and glandular plants, we run field experiments by manipulating the presence of the spider *P. flava* (Keyserling) 1877 on *Rhynchanthera dichotoma* (Lam.) D.C. (Melastomataceae), a shrubby plant that bears glandular trichomes. In some swamp sites from southeastern Brazil, *P. flava* occurs strictly on this glandular plant species (Morais-Filho & Romero 2008), representing a suitable system to test cost/benefit relationships in spider-plant interactions, as well as to investigate the role of glandular trichomes as mediators of mutualism between arthropods and plants. The main questions addressed in this study were: (1) Does *P. flava* suppress arthropods and decrease rates of herbivory in *R. dichotoma*? (2) Is this effect consistent over time? (3) Does the spiders decrease or increase plant fitness? (4) The spider benefits to occur on the glandular trichomes of *R. dichotoma*?

Material and methods

STUDY AREAS AND ORGANISMS

The field experiments were done in some swamp areas (20°48'-20°50'S; 49°16'-49°20'W; 494-542 m a.s.l.) at the margins of dams or streams near the city of São José do Rio Preto, northwestern São Paulo state, southeastern Brazil. The climate of the region is the type Cwa-Aw of Köppen, characterized by a season hot and humid in summer (November to March) and drought in winter (June to September). The annual rainfall varies from 1100 to 1250 mm with the rainy season getting 85% of annual rainfall (Barcha & Arid 1971). Climate data were collected from a meteorological station at 7 Km from the place of study.

The plant *Rhynchanthera dichotoma* (Melastomataceae) is a shrub (0,5-2,0 m height) that occurs in temporary aquatic ecosystems (Pinheiro 1995). This species has abundant glandular trichomes in stems and leaves, and blooms only once a year between March and May, soon after the rainfall season (Morais-filho & Romero 2009); the flowers are arranged in raceme-like inflorescences. The flowers are visited by Lepidoptera spp. and mainly by some bees of the genus *Bombus* and of tribes Meliponini and Euglossine (J.C. Morais-Filho, personal observation). Although this species is self-compatible (evidenced by manual pollination), it only produces seeds in the presence of pollinators; the vibration on anthers caused by pollinators is necessary for pollen release and to its adherence in the stigma (Pinheiro 1995). Its reproduction is explosive and synchronous, i.e., all individuals of a population having only vegetative branches can produce reproductive branches in less than 10 d. This plant species is often inhabited by different guilds of arthropods, including phytophages (e.g., Aphididae sp., Cicadellidae sp., Curculionidae sp., Chrysomelidae sp., Miridae sp., and larvae of Lepidoptera spp.), and predators (spiders and Reduviidae). Also, many insects are eventually adhered to glandular trichomes (e.g., Formicidae spp., Chironomidae sp., Aphididae sp.) (Morais-Filho & Romero 2008, 2009). Larvae of Geometridae sp., Chrysomelidae sp., and especially larvae and adults of Curculionidae sp., which occur in great abundance and also attack flower buds, cause the damages on leaves. Larvae of Lepidoptera spp. attack buttons and fruits, while Chrysomelidae sp. attacks only petals and stamens. Eventually, *Attini* sp. ants can also attack leaves and flowers (J.C. Morais-Filho, personal observation).

The spider *Peuceetia flava* occurs strictly on this plant species, where it forages and reproduces (Morais-Filho & Romero 2008, 2009). Its diet is variable, and includes Cicadellidae sp., larvae of Curculionidae sp., nymphs and adults of Miridae sp., Chrysomelidae sp., Formicidae spp., Pentatomidae sp., Pollinators (Euglossine bees), other

predators (spiders and Reduviidae), and small arthropods attached to glandular trichomes, as Formicidae spp., Chironomidae sp. and Aphididae sp. (Morais Filho & Romero 2008b). Individuals of *P. flava* are errant and do not build web; the females can reach about 12 mm long and males about 9 mm. Using its silk, females join the sides of two or three leaves to produce a ceiling-like shelter, under which it deposits an egg sac and remain for several days on it, apparently exhibiting maternal care (J.C. Morais-Filho, personal observation).

ABUNDANCE OF ARTHROPODS AND LEAF HERBIVORY

To investigate the effects of spiders on the abundance of arthropods and leaf herbivory, we randomly selected naturally growing plants of *R. dichotoma* using a systematic design (Hurlbert 1984), i.e., these plants were sequentially numbered according to the order of find along the margin of the stream and then were subjected to two treatments: the odd plants received spiders (experimental treatment) and even plants had the spiders removed (control treatment). Through daily inspections between 8:00 am and 12:00 pm, spiders were included or removed from the plants according to the treatment. The density of spiders on these plants was controlled based on its natural density in the field (~ one spider/branch, J.C. Morais-Filho, personal observation).

The experiment to test the effect of spiders on the abundance of arthropods associated to *R. dichotoma* occurred between December 2005 and March 2006. All the arthropods on the experimental (n = 21) and control plants (n = 21 plants) were counted 30, 60, and 100 days after the beginning of the experiment. The plants were inspected between 9:00 am and 13:00 pm; some arthropods were collected for identifications, but most of them were morfospeciated and identified in the field. Each plant was inspected around 5-7 min.

If *Peuceitia* removes phytophages from the leaves, they can potentially decrease leaf herbivory. However, this benefit could be variable in different seasons. To test these hypotheses we conducted an experiment in the rainy season (from December 2005 to February 2006) and another at the end of the rainy season (April 2006). For the first and second experiments, we used 44 and 34 plants, respectively. For each individual of *R. dichotoma*, we estimated leaf herbivory by randomly selecting and marking 3 to 5 young leaves (unexpanded) with thin colored wires placed on the basis of its petiole. Data on total leaf area and leaf area damaged by phytophages were estimated by using a clear plastic grid. For the first experiment, data were collected on four sampling dates following repeated measures design; the first sampling occurred at the beginning of the experiment (pre-treatment) and the reminders at intervals of 20 to 30 days until the end of the experiment. For

the second experiment these data were collected in two samples with 20 d intervals, following a repeated measures design.

FLORAL HERBIVORY AND SEED SET: A COST/BENEFIT ANALYSIS

Peucetia flava may reduce levels of herbivory on flower buds and flowers in anthesis of *R. dichotoma*, and consequently increase plant fitness. To test the effects of spiders on floral herbivory and plant fitness (i.e., seed set), we run an experiment during the reproductive season of *R. dichotoma* (April 2008) using 15 pairs (blocks) of randomly chosen plants following a randomized block design. One plant of the pair was randomly selected to receive spiders (experimental treatment) and the other had spiders removed (control treatment). A distance of 1–2 m separated paired plants, and each pair was at least 7 m apart from conspecifics. We used the same procedure for the maintenance of spiders as described above.

We randomly selected and marked 2-4 groups of buds per plant of the block, totalizing 134 groups in the experiment. Each group had 28.3 ± 1.2 buds (mean \pm 1 SE). These groups were monitored throughout the development of buds until the formation of fruits. Data on total number of flower buds and flowers in anthesis per group, and number of buds and flowers that had any herbivory damage, were obtained in 5 sampling dates at intervals of 5 days. During these samples we observed few arthropods and little damage in fruits, so these data were disregarded from the analysis. Since many of the flower buds have become fruit before the end of the experiment, data on the last two sampling dates were removed from the analysis to avoid missing values and loss in degrees of freedom. However, these data were plotted in figures.

At the end of the experiment, we randomly collected 10 fruits in the initial phase of development from each experimental plant ($n = 26$ plants). The fruits of each plant were stored in polyethylene tubes with lids made by mesh to allow drying and ripening. Then, these fruits were dissected to extract and count the seeds under a stereomicroscope (Bel Photonics®, Italy).

ROLE OF GLANDULAR TRICHOMES TO THE SPIDERS

To test whether glandular trichomes of *R. dichotoma* retain arthropods by their adhesive action, we conducted an experiment in August 2008 using eleven pairs (blocks) of *R. dichotoma* plantlets (0.4-0.6 m height) having a single branch. Each plant of the block was randomly designed to receive one of the following treatments: (1) removal of glandular trichomes from both sides of all the leaves (experimental treatment), or (2) glandular

trichomes remained intact (control). Experimental plants had most of the glandular trichomes carefully removed using blade-shave, while the controls were slightly shaken to simulate removal of trichomes. A distance of 0.5-1 m separated paired plants, and each pair was at least 5 m apart from conspecifics. To simulate insects that naturally adhere to the glandular trichomes, we used live *Drosophila melanogaster* vestigial flies; 30 flies were thrown at a height of 0.15 m above each plant of the experiment. Then, we counted the number of retained flies during its application, and 20, 40, 60 and 80 min after its application.

To test whether spiders select plants of *R. dichotoma* with glandular trichomes intact than those in which these structures were removed, we used 10 of the 11 pairs of plants of the previous experiment. Prior to the beginning of this experiment, all arthropods on the leaves of all the plants were removed. Then, a subadult or adult female spider (see classification in Morais-Filho & Romero 2008, 2009) of *P. flava* was introduced on each plant. The residence time (in hours) of spiders on these plants was determined.

Romero *et al.* (2008) observed that *P. flava* and *P. rubrolineata* spiders can feed on dead insects adhered to the glandular trichomes of *Trichogoniopsis adenantha* (Asteraceae); therefore, these spiders can also act as scavengers in this spider-plant system. To test whether *P. flava* feed on arthropods attached to glandular trichomes and with which frequency they feed on live and dead prey, we developed an experiment in December 2007 using live and dead flies of *D. melanogaster* isotopically labeled (^{15}N). The flies were labeled (ca. 10 atoms % excess) following the same procedures described in Romero *et al.* (2006). Prior to the beginning of the experiment, 15 live flies were applied in each of nine plantlets of *R. dichotoma* (0.4-0.6 m height) chosen randomly, while other nine plantlets received each 15 dead flies. Both live and dead flies were etherized in the field prior to the experiment, but some flies were etherized to death. To avoid traces of ether in the flies, the experiment began only a few minutes after the adherence of the flies on trichomes. Then, each plant received a subadult or adult female spider (see classification in Morais-Filho & Romero 2008, 2009) of *P. flava*, which remained for 3 days on it; to prevent escape of these spiders from the plants, we applied mesh cages above the plants. Prior to the beginning of the experiment, all plants were inspected and arthropods (dead or live) on the plants were removed. At the end of the experiment individuals of *Peuceetia* as well as *D. melanogaster* were collected, frozen and dried for isotopic analysis. $\delta^{15}\text{N}$ values were determined in the Stable Isotope Facility at the University of California at Davis. Stable isotope ratios of ^{15}N were determined by continuous flow isotope ratio mass spectrometer (IRMS) (20-20 mass spectrometer, PDZ Europa, Sandbach, England) after sample combustion to N_2 at 1000°C by an on-line elemental

analyzer (PDZ Europa ANCA-GSL). $\delta^{15}\text{N}$ values below 10 represent natural abundance of ^{15}N ; thus, only the spiders that have higher values actually ate labeled flies.

STATISTICAL ANALYSES

The total number of arthropods and arthropod number of each taxonomic group were compared between treatments (presence or absence of spiders) using repeated-measures ANOVA, with treatment (two levels) as a fixed factor and time as a factor of repetition. Leaf herbivory in both experiments (rainy season and end of rainfall) was compared using repeated-measures ANCOVA with treatment presence or absence of spiders (two levels) as fixed factor, time as repeated factor and initial number of leaves per plant as covariate for both experiments.

Data on proportion of damaged flower buds and flowers, and number of retained *Drosophila melanogaster* vestigial in plants with and without trichomes, were compared using randomized-block, repeated-measures ANOVA with treatment presence or absence of spiders (two levels) as fixed factor, time as repeated factor and blocks treated as random effects. Number of seeds per fruit was compared using randomized-block ANOVA with treatment presence or absence of spiders (two levels) as fixed factor and blocks treated as random effects. Residence time (in hours) of spiders on plants with and without trichomes was analyzed by randomized-block ANOVA with treatment presence or absence of trichomes (two levels) as fixed factor and blocks treated as random effects. $\delta^{15}\text{N}$ values from spiders that feed on dead or live labeled flies were compared using t-test.

When necessary, prior to analysis the data of counts were log or $\log(n+1)$ transformed, and data on proportions were arc-sine square root transformed for normalization and equalization of variances.

Results

ABUNDANCE OF ARTHROPODS AND LEAF HERBIVORY

The total number of arthropods on *R. dichotoma* decreased significantly over the experiment. However, this phenomenon is not related to the presence of spiders (Table 1, Fig. 1a). The number of Curculionidae sp., which represents the most abundant arthropods on these plants, also decreased significantly during the experiment without being affected by the spiders. In contrast, the number of larvae of Lepidoptera spp., Miridae sp. and Cicadellidae sp. were reduced in the presence of the predator (Table 1, Fig. 1).

In the rainy season the spiders had no apparent effect on the rates of leaf herbivory in *R. dichotoma*. In contrast, in the post-rain period leaf herbivory on plants with spiders decreased by 74% (Table 2, Fig. 2). In the rainy season the number of leaves increased by 47% (repeated-measures ANOVA: time: $F_{2,66} = 15.89$, $P < 0.001$); there was no influence of spiders in the production of leaves (repeated-measures ANOVA: treatment x time: $F_{2,66} = 0.72$, $P = 0.488$). In the period after the rain the number of leaves did not vary over time (repeated-measures ANOVA: $F_{1,29} = 1.52$, $P = 0.226$), and again the spiders had no influence on leaf production (repeated-measures ANOVA: treatment x time: $F_{1,29} = 1.42$, $P = 0.242$).

FLORAL HERBIVORY AND SEED SET: A COST/BENEFIT ANALYSIS

Peucetia flava spiders reduced by 85% the proportion of damaged flower buds (Table 3, Fig. 3a). The damages found in buds were typically small holes or buds eaten entirely. The presence of spiders also reduced by 55% the proportion of damaged flowers in anthesis (Table 3, Fig. 3b). Small holes in the calyx and petals, stamens partially eaten or flowers eaten entirely characterized the damage on flowers. Although we have not seen those responsible for this damage, we suspect that larvae and adults of Curculionidae sp. caused the holes found on buds and calyx of flowers; damages found on petals and stamens were probably caused by Chrysomelidae sp.; larvae of Lepidoptera spp. probably ate such structures entirely. During the reproductive season of *R. dichotoma*, the production of flower buds is continuous; each group marked had reproductive structures in different phenological phases. Consequently, in each new sampling period we counted new buds and flowers. This likely diluted the number of damaged structures observed, which explains the reduction in the proportion of herbivory on buds and flowers seen in Fig. 3.

Although the spiders have decreased the rates of floral herbivory, the number of seeds per fruit produced in plants with spiders (mean \pm 1 SE, 62.5 ± 9.5) and without spiders (65.1 ± 10.6) did not differ statistically (randomized-block ANOVA: $F_{1,12} = 0.20$, $P = 0.663$). Furthermore, no apparent damage was observed on the seeds counted.

ROLE OF GLANDULAR TRICHOMES TO THE SPIDERS

Soon after the application of *Drosophila vestigial* on the experimental plants, a greater number of flies was retained in plants of *R. dichotoma* that had intact glandular trichomes (mean \pm 1 SE: 19.9 ± 1.5) than those with trichomes removed (15.2 ± 1.2) (Table 4, Fig. 4). The significant interaction between treatment and time factor (Table 4) can be

explained by the difference of the initial number of flies trapped between experimental and control plants, and because this number decreased differentially between the treatments throughout the experiment (Fig. 4). *Peucetia* spiders remained for 4.4 times longer on plants with glandular trichomes intact (191.8 ± 43.1 hours) than on plants with trichomes removed (43.2 ± 19.8) (randomized-block ANOVA: $F_{1,9} = 9.03$, $P = 0.015$); some spiders remained on the plant with glandular trichomes intact for up to 314 hours (13 days).

The mean $\delta^{15}\text{N}$ values of spiders that had contact with dead and live flies did not differ statistically (t test: $F_{1,16} = 0.32$, $P = 0.577$), indicating that these spiders may act as predators or scavengers on this spider-plant system. Of the total number of spiders in treatments with live ($n = 9$) and dead *Drosophila* ($n = 9$), six and seven spiders fed on labeled *Drosophila*, respectively (Fig. 5).

Discussion

Peucetia flava decreased the abundance of many phytophagous insects, including Miridae sp., Cicadellidae sp. and larvae of Lepidoptera spp. These results show that the effect of the spiders on the arthropods is taxon-specific. Similar results were obtained by Romero *et al.* (2008), who showed that only organisms that tended to be more sessile (e.g., larvae of Lepidoptera, Miridae), but not those more active (e.g., *Melanagromyza* sp., Agromyzidae), were affected by the spiders *P. flava* and *P. rubrolineata*. However, in our study *P. flava* did not affect the population of Curculionidae sp., a typically sessile organism and the most abundant on *R. dichotoma*. Once they are easily found on the leaves of *R. dichotoma* and apparently have no kind of camouflage or cryptic coloration, we suggest that this beetle likely display some kind of physical or chemical defense against predation by *Peucetia*. Effective prey suppression of various insect groups by *P. flava* likely occurred because members of *Peucetia* genus (e.g., *P. viridans*) are generalists and feed on almost all arthropods present on plants (Nyffeler, Dean, & Sterling 1987, 1992; Nyffeler, Sterling & Dean 1992).

Although *P. flava* effectively removed phytophagous insects in the rainy season, this predator had no influence on leaf herbivory caused by insects during this season. In contrast, in the post-rain period spiders greatly decreased the rate of leaf herbivory in *R. dichotoma*. Our results indicate that the role of spiders as plant bodyguards is temporally conditioned. During the rainy months the rate of production of new leaves in *R. dichotoma*, added to the rapid expansion of these leaves, were high, a phenomenon likely triggered by bottom-up forces (e.g., rain, mineral input) that improved productivity of the swamp ecosystem. Higher

leaf productivity likely supported more herbivores and exceeded their capacity of leaf consumption, thus dampening top-down effects of spiders on herbivory. Similar results were reported by Denno, Gratton, Döbel & Finke (2003) by manipulating plant nutrition and presence of spiders in salt marsh islets from USA. In contrast, in the post-rain period the plant invests in the production of reproductive branches, and leaf productivity ceases. This allowed a longer exposure time of the spider and herbivores on leaves thus strengthen top-down effects of spiders in the system. Therefore, the conditional outcome in the spider-plant mutualism may have occurred because bottom-up forces dampened the effects of spiders in the rainy season.

The spiders *P. flava* greatly reduced damages on buds and flowers of *R. dichotoma*. However, they did not indirectly affected plant seed set. Thus, in this system *P. flava* improved plant reproduction with no indirect costs to plant fitness. To date, of the ten spider species of the genus *Peucetia* that live on glandular plants (Vasconcellos-Neto *et al.* 2007), three (i.e., *P. viridans*, *P. rubrolineata* and *P. flava*) were already considered mutualistic (Louda 1982, Romero *et al.* 2008, the present study). However, in contrast to our study, Louda (1982) and Romero *et al.* (2008) showed that the spiders *Peucetia* reduced or tended to reduce seed set on their host plants (Asteraceae). Contrasting responses of *Peucetia* on their host plants are likely related to types of pollinators and inflorescence architectures. For example, the main pollinator agents in *R. dichotoma* are bees of the genus *Bombus*, which are too big to be captured by *P. flava* (see also Pinheiro 1995). In fact, Dukas & Morse (2003, 2005) observed that success in capture of larger prey by *Misumena vatia* (Thomisidae) is low. In contrast, floral visitors of *T. adenantha*, for example, are smaller and can be captured by spiders (Romero *et al.* 2008). Moreover, in *Haplopappus venetus* (Asteraceae) the capitula are arranged side by side at the top of the inflorescence (flat-topped inflorescence) (Louda 1982), allowing the spiders *P. viridans* to forage on a larger number of capitula simultaneously. In *T. adenantha* the capitula are distant from each other, however, the spiders *P. flava* and *P. rubrolineata* can unite them likely to increase the foraging area (Romero *et al.* 2008). In contrast, in *R. dichotoma* the flowers are large and well spread, preventing these spiders to forage simultaneously on a large number of flowers, thus avoiding the reduction in the number of seeds produced. Thus, prey size and inflorescence architecture seem to determine the strength of the mutualisms involving *Peucetia* and glandular plants.

Whereas taxonomic groups closely related to *P. flava* are composed by web building spiders (e.g., *Tapinillus*; Santos 2004) and use these structures for prey capture, *P. flava* does

not build webs and forage actively on the vegetation. Once *Peucetia* selected plants having glandular hairs over others without such structures (see also Romero *et al.* 2008), and can capture arthropods adhered to them, we suggest that glandular trichomes may function analogously to webs by capturing small insects (e.g., Chironomidae). In fact, we showed that plants with glandular trichomes retain more prey than plants without trichomes. In the field, we observed *P. flava* feeding on Formicidae spp., Chironomidae sp. and Aphididae sp. attached to such structures. In addition, our experiments showed that *P. flava* can use both live and dead prey adhered to glandular trichomes, thus reinforcing that spiders of this genus can be predators, but also scavengers (Romero *et al.* 2008). Romero *et al.* (2008) suggested that the scavenger habit could mean an adaptation to periods of food scarcity. Since several arthropods die after becoming attached to glandular trichomes, if used by spiders can mean an extra source of energy, which is important for survival in this period. In fact, we observed that number of individuals of *P. flava* was high even in harsh seasons (Morais-Filho & Romero 2009). These results suggest that *Peucetia* may have specialized to forage on glandular plants because such adhesive structures contribute to spider nutrition, increasing the chance to find and capture prey without additional costs to produce webs.

To establish mutualisms involving spiders and plants, the spiders should be intimately associated to specific plant species or types of plants (Romero *et al.* 2008), and such associations should be stable spatiotemporally. And for specific associations to occur, plants must have structures that increase spider fidelity, providing them higher chances of prey capture, shelter, and/or nursery (Romero & Vasconcellos-Neto 2005a, b, c). Glandular trichomes seem to be a plant attribute that encourages persistence of *Peucetia* on plants. For example, *P. flava* occurs on glandular plants over a large geographic region from South America (Vasconcellos-Neto *et al.* 2007), and dynamics of their populations are relatively stable seasonally (Morais-Filho & Romero 2009). Therefore, glandular trichomes likely increase spider-plant fidelity spatiotemporally, although strong bottom-up forces seem to dampen the effects of spiders as plant bodyguards (see above).

We conclude that glandular trichomes mediate a facultative mutualism between *P. flava* and *R. dichotoma*, and seem to maintain this interaction stable spatiotemporally. Glandular trichomes likely exert an analogous effect of a web by retaining small insects and thus reducing spider energy expenditure on prey subjugation and capture. Besides, *Peucetia* can act as scavengers by feeding on dead arthropods stuck on the glandular trichomes. However, it still remains unclear whether *Peucetia* spiders have adaptations to live on

glandular hairs. The effects of spiders as plant bodyguards were temporally conditional likely because strong bottom-up forces (i.e., increased vegetative productivity in the rainy season) dampened top-down effects. In a cost/benefit analysis, in this system the presence of spiders was only beneficial. Once interactions involving *Peucetia* and glandular plants are spread worldwide, this protective mutualism may be quite common, but only now are being identified and investigated.

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Table 1. Repeated-measures ANOVA examining the effect of the presence of spiders on the number of arthropods/leaf on plants of *R. dichotoma*. Treatment = presence vs. absence of spiders; Time = sampling periods. Significant *P* values are boldfaced.

Source of variation	df	MS	<i>F</i>	<i>P</i>
Total arthropods				
Treatment	1	0.0015	2.99	0.095
Error	27	0.0005		
Time	2	0.0057	13.51	<0.001
Time x Treatment	2	0.0003	0.63	0.537
Error	54	0.0004		
Cicadellidae sp.				
Treatment	1	0.0000	4.33	0.047
Error	27	0.0000		
Time	2	0.0000	0.02	0.975
Time x Treatment	2	0.0000	1.92	0.157
Error	54	0.0000		
Curculionidae sp.				
Treatment	1	0.0000	0.14	0.709
Error	27	0.0003		
Time	2	0.0020	10.44	<0.001
Time x Treatment	2	0.0003	1.69	0.194
Error	54	0.0002		
Larvae of Lepidoptera spp.				
Treatment	1	0.0000	10.57	0.003
Error	27	0.0000		
Time	2	0.0000	0.32	0.729
Time x Treatment	2	0.0000	0.43	0.655
Error	54	0.0000		
Miridae sp.				
Treatment	1	0.0001	6.80	0.015
Error	27	0.0000		
Time	2	0.0001	8.57	<0.001
Time x Treatment	2	0.0000	0.80	0.455
Error	54	0.0000		

Table 2. Repeated-measures ANCOVA examining the effects of spiders on the leaf herbivory in *R. dichotoma* during the rainy season and post-rain period. Treatment = presence vs. absence of spiders; Time = sampling periods. Significant *P* values are boldfaced.

Source of variation	df	MS	<i>F</i>	<i>P</i>
Foliar herbivory; rainy season				
Treatment	1	0.0000	0.01	0.938
No. of leaves (cov)	1	0.0067	1.60	0.224
Error	16	0.0042		
Time	3	0.0042	2.51	0.070
Time x Treatment	3	0.0007	0.41	0.747
Time x No. of leaves	3	0.0012	0.74	0.531
Error	48	0.0017		
Foliar herbivory; post-rain				
Treatment	1	0.0174	8.54	0.006
No. of leaves (cov)	1	0.0031	1.51	0.229
Error	31	0.0020		
Time	1	0.0099	5.64	0.024
Time x Treatment	1	0.0166	9.49	0.004
Time x No. of leaves	1	0.0015	0.83	0.370
Error	31	0.0017		

Table 3. Randomized-block, repeated-measures ANOVA examining the effects of the presence of spiders on herbivory of flower buds and flowers in anthesis of *R. dichotoma*. Treatment = presence vs. absence of spiders; Time = sampling periods. Significant *P* values are boldfaced.

Source of variation	df	MS	<i>F</i>	<i>P</i>
Herbivory in flower buds				
Treatment	1	1.5834	20.44	<0.001
Block	12	0.0352	0.45	0.907
Error	12	0.0775		
Time	2	0.2001	2.07	0.148
Time x Treatment	2	1.7804	18.42	<0.001
Time x Block	24	0.0575	0.59	0.895
Error	24	0.0967		
Herbivory in flowers in anthesis				
Treatment	1	0.6364	5.88	0.031
Block	13	0.2320	2.14	0.091
Error	13	0.1083		
Time	2	0.5563	5.81	0.008
Time x Treatment	2	0.5321	5.55	0.010
Time x Block	26	0.0636	0.66	0.849
Error	26	0.0958		

Table 4. Randomized-blocks, repeated-measures ANOVA examining the effects of the presence of glandular trichomes in the retention of *D. melanogaster* vestigial flies on leaves of *R. dichotoma*. Treatment = presence vs. absence of glandular trichomes; Time = sampling periods. Significant *P* values are boldfaced.

Source of variation	df	MS	<i>F</i>	<i>P</i>
Treatment	1	1.6620	11.19	0.007
Block	10	0.3743	2.52	0.081
Error	10	0.1486		
Time	4	1.3925	60.36	<0.001
Time x Treatment	4	0.0911	3.95	0.008
Time x Block	40	0.0466	2.02	0.014
Error	40	0.0231		

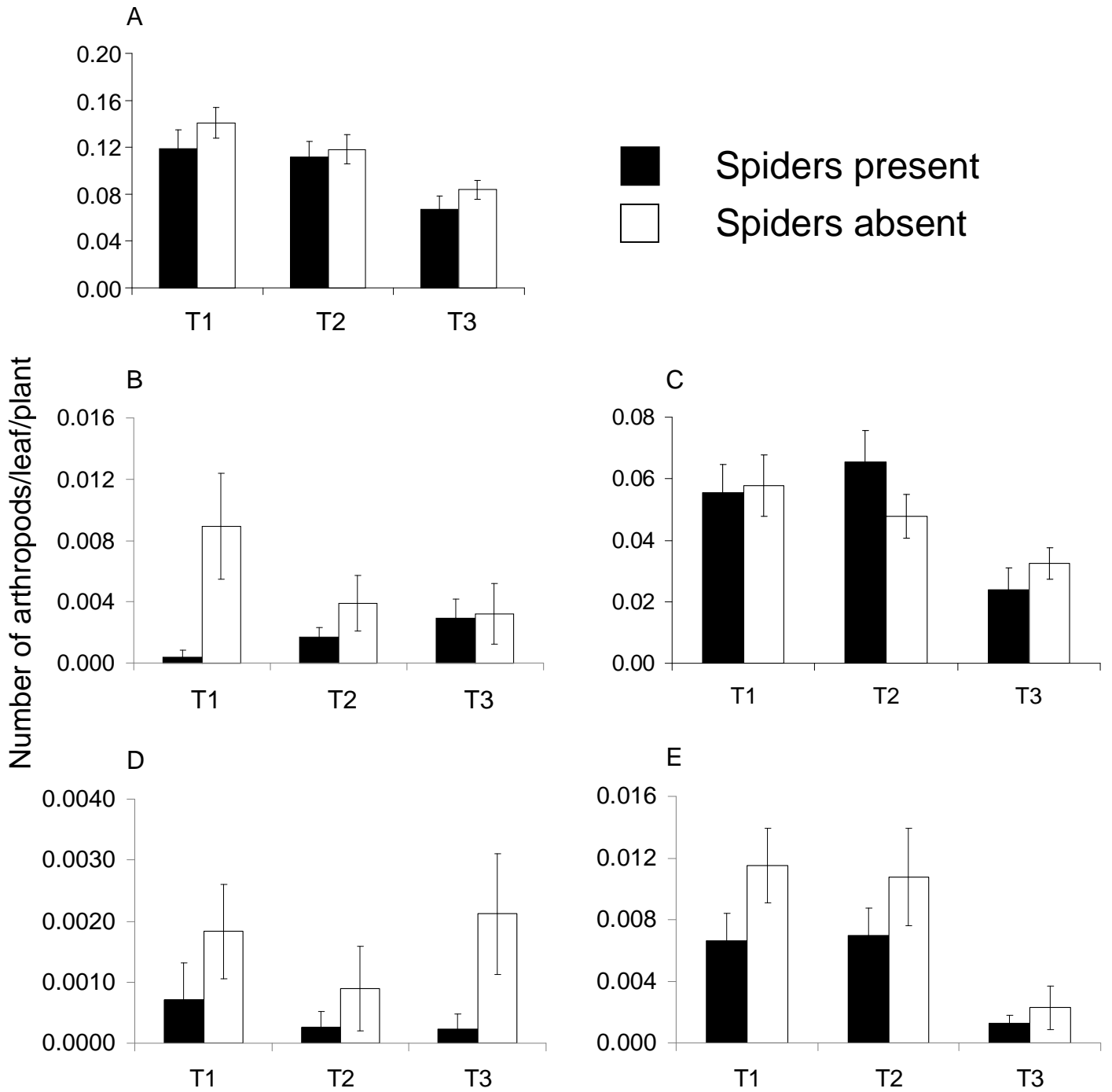


Figure 1. Total number of arthropods (A), Cicadellidae sp. (B), Curculionidae sp. (C), larvae of Lepidoptera spp. (D), and Miridae sp. (E) on *R. dichotoma* in the presence and absence of *P. flava* spiders. Error bars represent ± 1 SE. Sampling dates: T1 = Jan 13, 2006; T2 = Feb 13, 2006; T3 = Mar 22, 2006

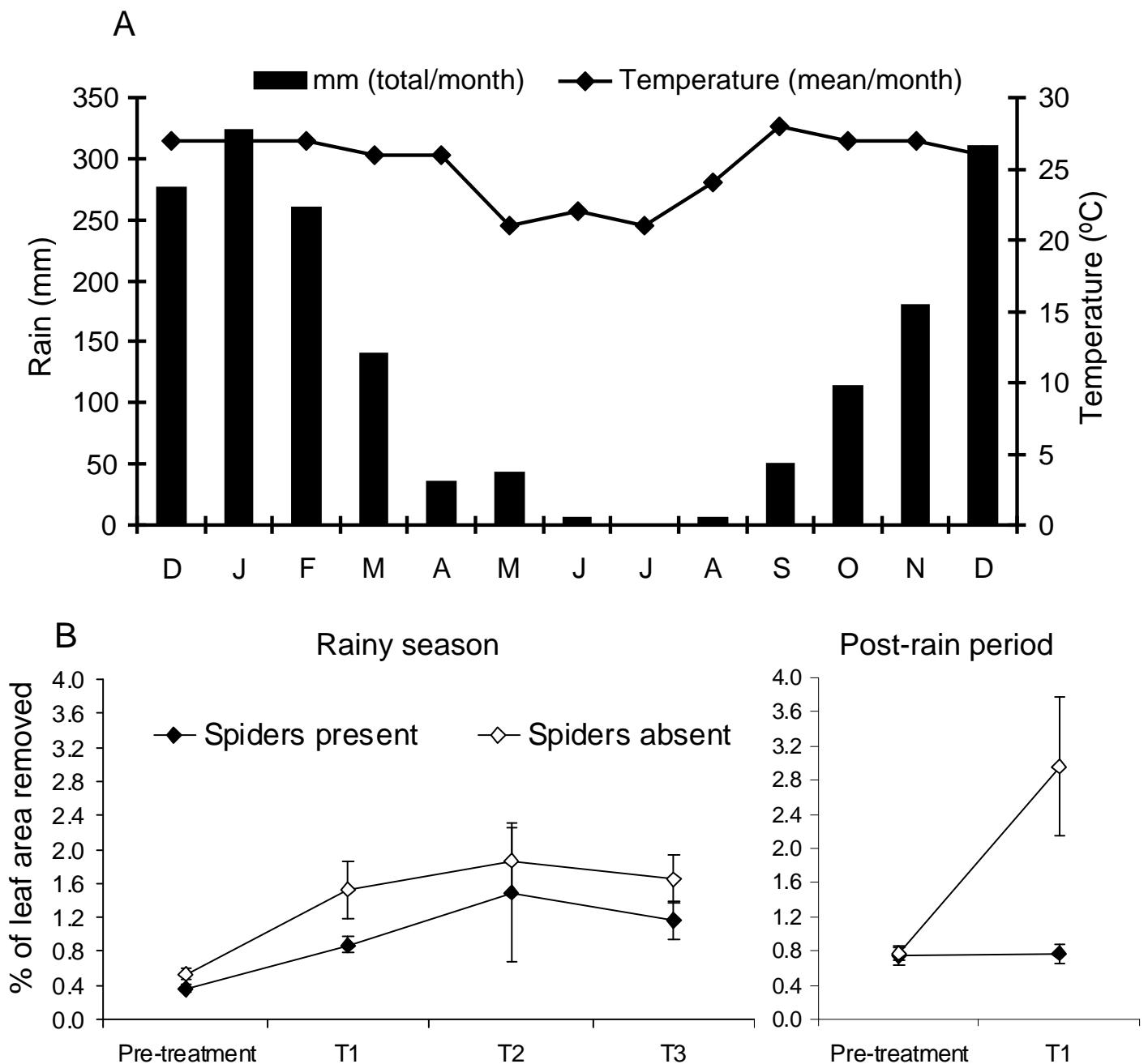


Figure 2. (A) Monthly rainfall and temperature variation over the experiments of leaf herbivory; (B) Mean percentage of leaf area damaged by chewing phytophages on *R. dichotoma* in the presence and absence of spiders, during rainy and post-rain periods. Error bars represent ± 1 SE. Sampling dates: (Rainy season) Pre-Treatment = Dec 13, 2005; T1 = Jan 12, 2006; T2 = Feb 02, 2006; T3 = Feb 22, 2006; (Post-rain period) Pre-Treatment = Apr 10, 2006; T1 = Apr 30, 2006.

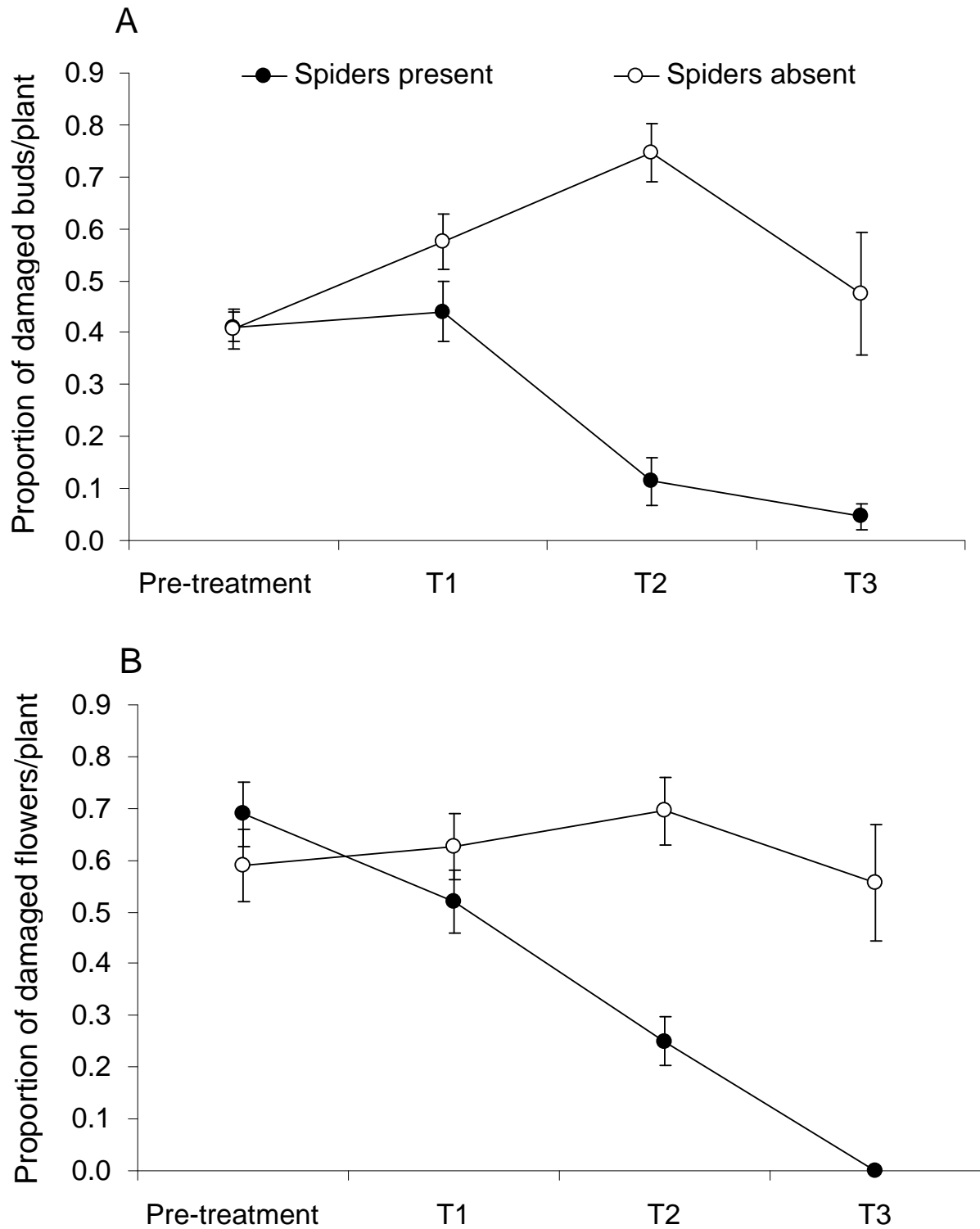


Figure 3. Mean proportion of damaged flower buds (A) and flowers in anthesis (B) of *R. dichotoma* in the presence and absence of spiders. Error bars represent ± 1 SE. Sampling dates: Pre-Treatment = Apr 08, 2008; T1 = Apr 13, 2008; T2 = Apr 18, 2008; T3 = Apr 23, 2008.

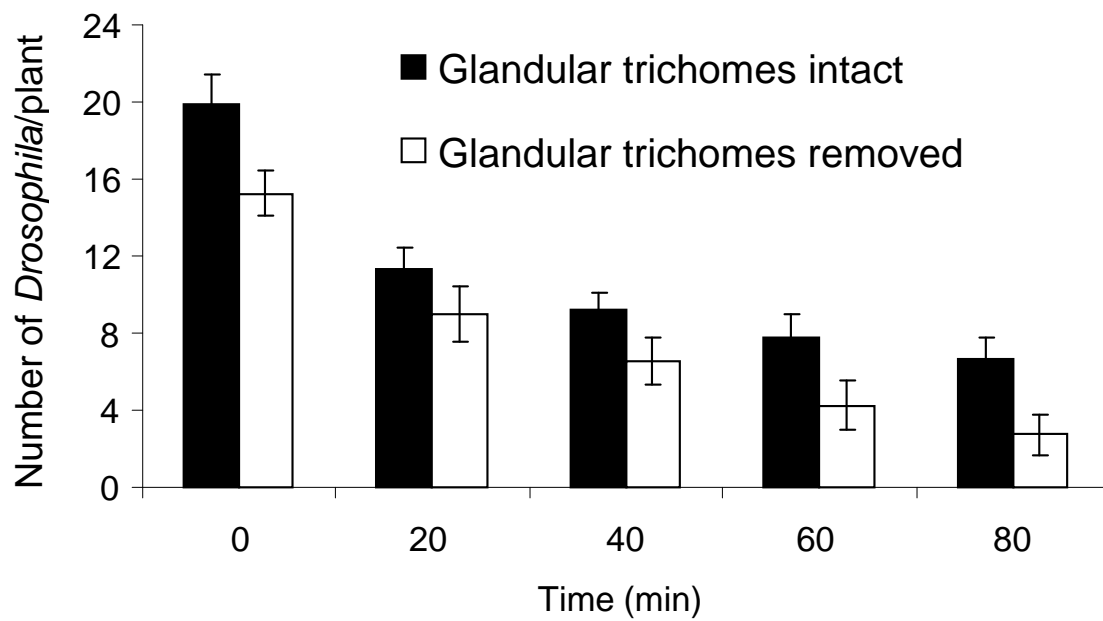


Figure 4. Mean number of *D. melanogaster* vestigial flies per plant on leaves of *R. dichotoma* with glandular trichomes intact and removed. Error bars represent ± 1 SE.

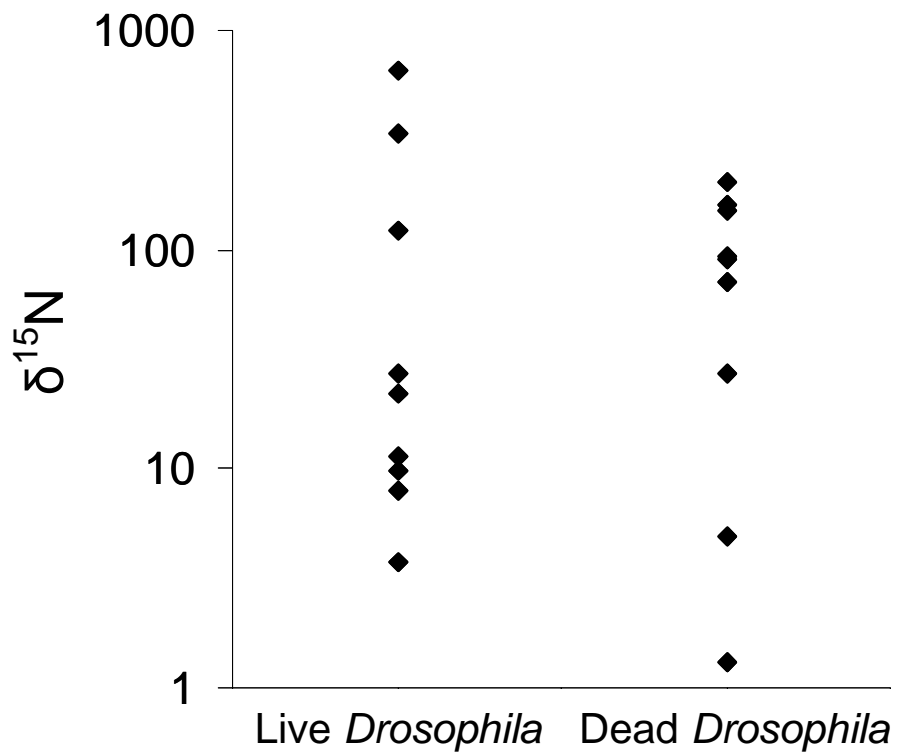


Figure 5. $\delta^{15}\text{N}$ values (log scale) of *P. flava* spiders that remained on plants that received live (n = 9 spiders) and dead (n = 9 spiders) labeled flies (^{15}N). The mean $\delta^{15}\text{N}$ value of the enriched flies was 1079 (n = 3).

3. ANEXO A

Morais-Filho, J.C. & Romero, G.Q. 2008. Microhabitat use by *Peucetia flava* (Oxyopidae) on the glandular plant *Rhynchanthera dichotoma* (Melastomataceae). *Journal of Arachnology* 36(2):374-378.

Microhabitat use by *Peucetia flava* (Oxyopidae) on the glandular plant *Rhynchanthera dichotoma* (Melastomataceae)

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Running head: MORAIS-FILHO & ROMERO – MICROHABITAT USE BY *PEUCETIA FLAVA*

ABSTRACT. Several studies have reported that plant structural components can exert strong influences on the density and distribution of spiders. However, little is known about which plant traits mediate specific associations between spiders and plants. In southeastern Brazil, the lynx spider *Peucetia flava* Keyserling 1877 (Oxyopidae) is commonly found on the plant *Rhynchanthera dichotoma* (Melastomataceae), a shrub that bears glandular trichomes. In this study we investigated if *Peucetia* occurs strictly on *Rhynchanthera* and what plant parameters influence the spiders' distribution. In addition, we recorded the vertical distribution of spiders of different ages in the plant canopy. Throughout the year *Peucetia* was observed only on the glandular plant *Rhynchanthera*, indicating that this association is specific and predictable. Statistical analysis showed no difference in the number of spiders between plants of *Rhynchanthera* with and without flowers, suggesting that this specific association is mediated by the presence of glandular trichomes, and not by reproductive structures. The distribution of *Peucetia* over the year was related to the number of arthropods on plants, as well as the number of leaves and height of the host plants, indicating that *Peucetia* probably choose sites of high food availability. Adults and subadults occurred on higher places on the crown than young and juveniles.

Keywords: Plant architecture, glandular trichomes, spider-plant interactions

INTRODUCTION

Spiders are among the most abundant and diverse arthropods on vegetation (Wise 1993; Foelix 1996; Romero & Vasconcellos-Neto 2006) and are strongly influenced by variations in plant architecture (Greenquist & Rovner 1976; Riechert & Gillespie 1986; Gunnarsson 1990, 1992, 1996; Romero & Vasconcellos-Neto 2005a). Moreover, spiders are recognized by their ability to choose microhabitats of better quality, i.e., they generally prefer those with high abundance of prey (e.g., reproductive branches) (Morse & Fritz 1982; Ward & Lubin 1993; Morse 2007). Yet, some spiders may choose substrata based on leaf morphology (e.g., Thomisidae, *Diaea*, Evans 1997). Although these studies reported spider selection for microhabitats, most of them refer to only a few taxonomic groups (e.g., Thomisidae, Salticidae, and Araneidae) (Romero & Vasconcellos-Neto 2006) and few studies

describe how plant parameters influence the density of hunting spiders (e.g., Romero & Vasconcellos-Neto 2005a).

Recent studies have reported specific associations of spiders with specific plant features (Figueira & Vasconcellos-Neto 1991, 1993; Arango et al. 2000; Rossa-Feres et al. 2000; Romero 2001; Romero & Vasconcellos-Neto 2003, 2004a, b, c, 2005a, b, c; Dias & Brescovit 2004). To date, the better studied examples of botanical structures that mediate spider-plant interactions are architecture in rosettes and glandular trichomes (Romero & Vasconcellos-Neto 2007; Vasconcellos-Neto et al. 2007). While the former facilitates the encounter of prey and mates and can be used as sites for egg-laying and shelter for adults and immatures, the later trap insects that can be used as prey by some spiders (Romero & Vasconcellos-Neto 2003, 2004a, 2005a; Vasconcellos-Neto et al. 2007).

Up to ten species of the genus *Peucetia*, including two South American species, *P. flava* Keyserling 1877 and *P. rubrolineata* Keyserling 1877 (Oxyopidae), live strictly associated with many species of glandular plants in Neotropical, Nearctic, Afrotropical, and Palearctic regions (Vasconcellos-Neto et al. 2007). However, few studies have investigated patterns of host plant use in *Peucetia*, especially which plant traits besides presence of glandular trichomes influence the distribution of spiders of this genus on their host plants (e.g., Louda 1982; Arango et al. 2000). In southeastern Brazil specimens of *P. flava* were reported to occur frequently on *Rhynchanthera dichotoma* (Lam.) DC. Clarke (Melastomataceae), a glandular shrubby plant that typically inhabits swamps (J.C. Morais-Filho & G.Q. Romero, personal observations). To better understand this system, the purpose of our study was to evaluate (1) if *Peucetia flava* occurs strictly on *Rhynchanthera* or randomly on any other plant species; (2) which plant parameters influence the distribution of this spider population; and (3) if there is some variation in the vertical distribution of *Peucetia* of different ages in the canopy of *Rhynchanthera*.

METHODS

Study area and organisms. – This work was done in a swamp along an affluent margin of a lake (altitude 494 m; 20°49'S, 49°20'W) in São José do Rio Preto city, northwest of São Paulo state, southeastern Brazil. The climate in this region is of the type Cwa-Aw of Köppen, characterized by a hot/rainy season in the summer and dry in the winter. The annual precipitation varies from 1100 to 1250 mm, receiving 85% of the rainfall in the rainy season (September – March) and only 15% in the cold/dry season (Barcha & Arid 1971).

Rhynchanthera dichotoma is a hydrophilic phanerogamic shrub (0.5-2.0 m high) that occurs in temporary aquatic ecosystems, and the flowering period of this plant occurs once a year between March and May. This plant is frequently habited by arthropods of various guilds, including phytophages (e.g., Curculionidae, Miridae, Aphididae, Homoptera) and predators (e.g., spiders, Reduviidae). Many insects (e.g., ants, Chironomidae, Aphididae) adhere to the glandular trichomes which are very dense on leaves and young stems of this plant species. The spider *Peucetia flava* is the most common predator on this plant and uses it as foraging and reproductive site (J.C. Morais-Filho & G.Q. Romero, personal observations).

Voucher specimens of the spiders collected (males and females) were deposited in the Arachnological Collection of the Laboratório de Artrópodes Peçonhentos, Instituto Butantan, São Paulo.

Fidelity of *Peucetia* for host plant.– Data were obtained in June 2007 in an area of 800 m² (two independent plots: 10 x 30 m and 10 x 50 m). We inspected leaves and recorded the presence or absence of *P. flava* on stems of 90 individuals of *Rhynchanthera* and another 250 plants without glandular trichomes, those belonging to diverse families (e.g., Asteraceae, Melastomataceae, Poaceae, Zingiberaceae).

Plant parameters and distribution of *Peucetia*.– To verify if *P. flava* is more abundant on plants with flowers than without flowers, in March-April 2006 and April 2008 (the flowering periods) we counted the number of spiders on 8-22 individuals of *Rhynchanthera* with flowers and on 14-27 individuals without flowers. For each plant we also counted the number of leaves. Data were log (n+1) transformed to equalize variances and then compared using ANCOVA, with presence or absence of flowers (treatment) as a fixed effect (2 levels), years (2006 and 2008) as a fixed effect (2 levels), and number of leaves as the covariate.

To verify what plant parameters influence *P. flava* distribution, we surveyed 16-32 plants monthly between December 2005 and December 2006. Data on plant height, number of leaves and flowers, and total number of arthropods (potential free prey and potential prey stuck to glandular trichomes) were assessed for each plant surveyed. We also recorded the number of *P. flava* of various ages. To test which plant parameters influence the distribution of spiders in each month over the year, we used multiple linear regressions (Zar 1996) with the total number of individuals of *Peucetia* as the dependent variable and the parameters plant height, number of leaves, flowers, and total number of arthropods as the independent variables. The multiple linear regression test concerning all these four independent variables detected multicollinearity. We then removed some independent variables following

procedures suggested by Zar (1996): we first ran a linear regression analysis between all these independent variables and selected those with the smallest value of r^2 (i.e., height, number of leaves, and total number of arthropods). By this selection we excluded the independent variable “abundance of flowers” that was strongly related to the other independent variables because *R. dichotoma* produce flowers only once, in a short period of the year.

Vertical distribution among age classes.– To test if there is some variation in the vertical distribution of *Peucetia* from different ages in the canopy of *Rhynchanthera*, we measured the body size of each spider and its proportional height in the crown of the plant. For this, we divided the height that the spider occupied in the crown by the height of the crown. We defined the height of the crown as the length between the highest tip of the plant and the base of the crown (i.e., the junction of the first secondary branch with the main trunk); thus a value close to zero means that the spider is at the base of the crown, and values close to one indicates that the spider is at the tip of the plant. To categorize the instars the spiders were classified as young [total body length (cephalothorax + abdomen) \leq 3.0 mm], juveniles ($>$ 3.0 mm but \leq 6.0 mm), subadults (females $>$ 6.0 mm but $<$ 9.0 mm; males $>$ 6.0 mm but \leq 7.0 mm, with a dilated palp and slightly orange abdomen) and adults (females \geq 9.0 mm; males $>$ 7.0 mm, with a dilated sclerotized palp and orange abdomen). Data on distribution of spiders of each age class were compared for each sampling period using ANOVA (Zar 1996). Prior to the analyses these proportions were arc-sin square root transformed for data normalizations. If necessary, we performed paired comparisons using Fisher’s LSD *post hoc* test. The test was run only in December 2005 because in this period the power of the performed test was high (95%); in the remaining months the power of the performed test was very low, varying from 5-35%.

RESULTS

Fidelity of *Peucetia* for host plant.– Although we have observed several spider species on plants that do not bear glandular hairs, *Peucetia flava* was observed only on the glandular plant *Rhynchanthera dichotoma*. In June (2007), we found 44 individuals of *P. flava* on *Rhynchanthera dichotoma* and none on the other plant species without glandular hairs.

Plant parameters and distribution of *Peucetia*.– There was no statistical difference in number of spiders between plants with and without flowers, and this was the case both in 2006 (mean \pm 1 SE; plants with flowers: 2.50 ± 0.56 spiders; plants without flowers: 1.37 ± 0.30 spiders) and 2008 (plants with flowers: 0.50 ± 0.19 spiders; plants

without flowers: 0.57 ± 0.17 spiders) (Table 1). The covariate (number of leaves) differed statistically (Table 1), indicating that the number of leaves, and not presence of flowers, determines spider distribution. Multiple linear regressions showed that the distribution of *Peucetia* over the year was related to the number of arthropods in December 2005, May and October ($P \leq 0.032$), as well as number of leaves in February and July ($P \leq 0.026$), and height of plants in December 2006 ($P < 0.001$) (Table 2).

Vertical distribution among ages classes.– In December 2005 adults and subadults of *Peucetia* occurred on higher sites on the crown than juveniles and young (Fig. 1; $F_{3,86} = 6.92$; $P < 0.001$).

DISCUSSION

Peucetia flava occurred only on *Rhynchanthera dichotoma*. This result suggests that in our study site the spider species is strictly associated with this glandular plant. On *R. dichotoma*, these spiders were frequently seen foraging, feeding and displaying reproductive behaviors; females produced egg sacs in almost all months (J.C. Morais-Filho & G.Q. Romero, unpublished data). These observations suggest that *Rhynchanthera* is a suitable microhabitat for *P. flava*. In addition, in northeast, southeast, and southern Brazil *P. flava* is reported to occur associated with sixteen glandular shrubs (Vasconcellos-Neto et al. 2007), thus reinforcing the hypothesis of a high fidelity of these spiders to glandular plants. The reason why *P. flava* is found associated with these plants may be due to the function of the glandular hairs as insect traps, which facilitate prey capture by trapping or preventing insects from dislodging themselves and escaping (Dolling & Palmer 1991; Ellis & Midgley 1996; Romero & Vasconcellos-Neto 2004a). In fact, *Peucetia flava* can feed on insects stuck to glandular trichomes of *Rhynchanthera* (e.g., ants, Chironomidae, Aphididae) (J.C. Morais-Filho personal observation) and Romero et al. (2008) showed that this spider can also feed on insects stuck to glandular trichomes of *Trichogoniopsis adenantha*. Furthermore, while glandular trichomes could benefit spiders by facilitating prey capture, the spiders preying on these plants may remove phytophagous insects thus also providing benefits to the plants. This hypothesis will be tested in future research.

Generally, spiders occur more frequently on plant parts that have flowers (reproductive branches), since these structures attract potential prey (pollinators) and are thus better quality sites (Louda 1982; Morse & Fritz 1982; Romero & Vasconcellos-Neto 2004a, 2006). However, this seems not to be the case for *P. flava*; although flowers of *R. dichotoma* attract potential prey of *P. flava*, there was no evidence that *P. flava* chose plants based on

presence of flowers. These results suggest that *P. flava* chose plants primarily based on presence of glandular trichomes, and not presence of flowers, and reinforces the assumption described above regarding the specific association of this species with glandular plants.

These results suggest that, in different periods of the year, *P. flava* may be choosing plants based on other characteristics such as the number of arthropods stuck on glandular trichomes, the number of leaves on the plant, or the height of the plant. Plants with more leaves may represent sites of better quality for foraging (larger surface area) and shelter (e.g., Gunnarsson 1990; Romero & Vasconcellos-Neto 2005b). In addition, since leaves of this plant bear glandular hairs able to trap insects, more leaves may mean higher probability of an insect adhering to these sticky structures. In fact, the number of leaves influenced the abundance of adhered arthropods on *R. dichotoma* (J.C. Morais-Filho & G.Q. Romero, unpublished data). Since *P. flava* and its congener *P. rubrolineata* can act as scavengers (Romero et al. 2008), being on plants with greater number of leaves may increase the chance to feed on dead insects stuck to glandular trichomes.

In USA and Mexico *Peucetia viridans* Hentz 1832 is reported to occur associated with the glandular plants *Haplopappus venetus* (Asteraceae) (Louda 1982) and *Cnidocolus aconitifolius* (Euphorbiaceae) (Arango et al. 2000), respectively. These authors reported that the spider selected the highest plants. Arango et al. (2000) found that *P. viridans* uses high-quality portions of its habitat, choosing those plants offering better sources of food, shelter, and favorable environmental conditions. The frequency of spiders on higher plants could be related to prey availability, as higher plants have a higher number of leaves.

Adults and subadults of *Peucetia flava* occurred on higher sites in the crown than juveniles and young. This distribution may confer an easy way for adults and subadults to migrate by ballooning between plants to search for sites of better quality. Alternatively, higher regions in the canopy may represent sites with higher prey availability. In contrast, younger individuals of *Peucetia* (i.e., juveniles and young) may have selected lower sites possibly as shelter, as well as to avoid competition or cannibalism with the larger conspecifics. In fact, we observed cannibalism in this spider population. In California, Turner (1979) reported that 5.8% of the diet of *P. viridans* was composed of other individuals of *P. viridans*. In contrast to our results, for the *P. viridans* – *C. aconitifolius* system, Arango et al. (2000) found no preference for location in the plant crown among instars. Thus, although it is expected that larger spiders occur on higher sites and smaller spiders occur on lower ones, this distribution pattern was inconsistent among spider-plant systems, as well as among different periods of the year for our system.

In conclusion, *Peucetia flava* occurred strictly associated with *Rhynchanthera dichotoma* probably due to the presence of glandular trichomes; it may benefit from insects adhering to these sticky structures. On this plant species *Peucetia* seemed to evaluate varying plant parameters depending on the period of the year, being affected mainly by abundance of leaves. Once upon a plant with more leaves, the spiders increase the chance of feeding on dead insects stuck to glandular trichomes through scavenging behavior. Juveniles and young *Peucetia* tended to occur on lower regions on the crown, possibly as a way to avoid competition and cannibalism with the larger conspecifics.

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Table 1. ANCOVA examining the influence of presence/absence of flowers (treatment) on *R. dichotoma* on the abundance of *P. flava*, during two reproductive periods of the host plant (years of 2006 and 2008). Significant *P* values are boldfaced.

Source of variations	df	MS	F	P
No. of leaves (cov)	1	1.3892	32.59	< 0.001
Treatment	1	0.0123	0.29	0.592
Year	1	0.0298	0.70	0.406
Year x Treatment	1	0.0371	0.87	0.354
Error	66	0.0426		

Table 2.–The coefficient (and *P* values in parenthesis) of multiple linear regressions between *P. flava* density (dependent variable) and plant height, number of leaves and total number of arthropods on the plant *R. dichotoma* in different periods of the year. Significant *P* values are boldfaced.

Months	Height	Leaves	Arthropods
December	0.74 (0.064)	0.32 (0.091)	0.27 (0.032)
January	-0.20 (0.674)	0.44 (0.090)	0.06 (0.793)
February	0.21 (0.676)	0.60 (0.003)	0.22 (0.117)
March	0.60 (0.362)	0.35 (0.182)	0.22 (0.143)
April	-0.90 (0.424)	0.81 (0.059)	-0.22 (0.496)
May	1.51 (0.348)	-0.23 (0.577)	0.59 (0.029)
June	0.45 (0.556)	0.37 (0.115)	-0.01 (0.942)
July	-0.13 (0.851)	0.60 (0.026)	-0.01 (0.952)
August	0.49 (0.440)	0.36 (0.208)	0.40 (0.080)
September	0.16 (0.768)	0.50 (0.075)	-0.02 (0.896)
October	0.57 (0.319)	-0.33 (0.236)	0.40 (0.023)
November	-0.48 (0.445)	0.63 (0.249)	0.18 (0.652)
December	1.17 (< 0.001)	0.21 (0.297)	0.19 (0.185)

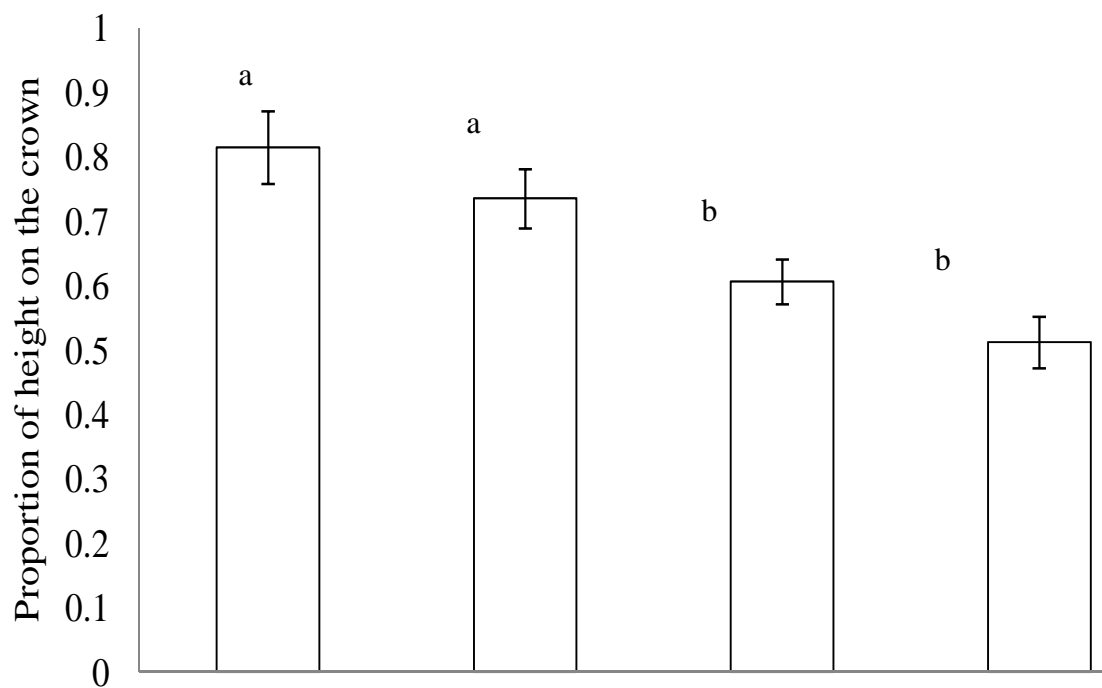


Figure 1.—Vertical distribution of spider age classes in December 2005. Different letters indicate statistical differences (ANOVA/Fisher LSD). Error bars indicate $\pm 1SE$. See age group definitions in Methods.

4. ANEXO B

Morais-Filho, J.C. & Romero, G.Q. 2009. Natural History of *Peucetia flava* (Araneae, Oxyopidae): seasonal density fluctuation, phenology and sex ratio on the glandular plant *Rhynchanthera dichotoma* (Melastomataceae). *Journal of Natural History* 43:701-711.

**Natural History of *Peucetia flava* (Araneae, Oxyopidae): seasonal density fluctuation,
phenology and sex ratio on the glandular plant *Rhynchanthera dichotoma*
(Melastomataceae)**

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Running title: Natural History of *Peucetia flava*

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Abstract

The seasonal density fluctuation, phenology and the sex ratio of *Peucetia flava* (Oxyopidae) on *Rhynchanthera dichotoma* (Melastomataceae) were investigated during a year in a swamp from southeastern Brazil. *P. flava* displayed an unusual non-seasonal life cycle and the population size varied few over the year. The density of *Peucetia* spiders increased with the increase in the abundance of leaves and arthropods adhered to glandular trichomes on *R. dichotoma* leaves. Our findings suggest that seasonal density fluctuation of *Peucetia* may be influenced by foraging sites availability (i.e., leaves) and prey supply (i.e., arthropods adhered to glandular trichomes). The unusual seasonal stability of *P. flava* may be related to the type of habitat in which this spider occurs (swamp), because of the constant input of allochthonous resources from water source, i.e., aquatic insects that migrate to terrestrial environment.

Keywords: *Peucetia*, animal-plant interactions, seasonal fluctuation, swamp, Neotropical

Introduction

Biotic and abiotic factors, such as temperature, rainfall, symbionts, competitors and natural enemies, as well as quality and quantity of resources, are important forces in natural systems, and thus can determine population dynamics and community structure through top-down (e.g., natural enemy impact) and bottom-up forces (e.g., resource limitation) (Price et al. 1980, Hunter and Price 1992, Denno et al. 2002, Gratton and Denno 2003). Spiders are among the most abundant and diverse arthropods on vegetation (Wise 1993, Foelix 1996, Romero and Vasconcellos-Neto 2007a) being frequently exposed to top-down and bottom-up forces in complex food webs (Spiller and Schoener 1990, 1994; Schmitz et al. 2000; Gratton and Denno 2003).

Several recent studies reported specific associations between spiders and plants (Figueira and Vasconcellos-Neto 1991, 1993; Arango et al. 2000; Rossa-Feres et al. 2000; Romero and Vasconcellos-Neto 2003, 2004a, b, c, 2005a, b, c; Dias and Brescovit 2004). For example, up to ten spider species of the genus *Peucetia* are associated with plants bearing glandular trichomes worldwide (Vasconcellos-Neto et al. 2007). However, to date few studies described the mechanisms and processes that act on the dynamics of these systems, including phenologies, food items and interactions between spiders and organisms of other trophic

levels in Neotropical regions (e.g., Arango et al. 2000; Romero and Vasconcellos-Neto 2003, 2005c). The phenology of an organism comprise the temporal variation in its life cycle and several studies sustain that spiders associated to plants adjust their phenology in response to seasonal variations of abiotic and biotic factors, such as rainfall (Arango et al. 2000; Rossa-Feres et al. 2000; Romero and Vasconcellos-Neto 2003) and prey availability (Arango et al. 2000; Romero and Vasconcellos-Neto 2004a).

Furthermore, interactions between biotic and abiotic factors are important in determining the structure of arthropod community associated with plants. For example, in the *Misumenops argenteus* (Thomisidae) – *Trichogoniopsis adenantha* (Asteraceae) system, Romero and Vasconcellos-Neto (2003) showed that with increased rainfall (i.e., bottom-up forces) the plant increases production of reproductive branches that subsequently supported populations of arthropods which, in turn, supported population of *M. argenteus*. Arango et al. (2000) described similar results in the *Peucetia viridans* – *Cnidocolus aconitifolius* system. In addition, *M. argenteus* showed to be effective in diminishing herbivore density, indicating that top-down forces also act to structure this spider-plant system (Romero and Vasconcellos-Neto 2004b, 2007b).

The spider genus *Peucetia* (Oxyopidae) occurs worldwide and comprises 46 species of small to medium sized spiders (Santos and Brescovit 2003; Platnick 2008) that actively hunts and capture a huge variety of prey on vegetation (Brady 1964; Louda 1982; Uetz et al. 1999). However, almost all the knowledge about ecology and behavior of this genus refer to populations of the green lynx spider *Peucetia viridans* Hentz (Brady 1964; Whitcomb 1962; Whitcomb and Eason 1965; Whitcomb et al. 1966; Randall 1977, 1982; Turner 1979; Louda 1982; Fink 1986, 1987; Willey and Adler 1989; Arango et al. 2000; but see Gonzaga et al. 1998, Dippenaar-Schoeman 2005, Vasconcellos-Neto et al. 2007), that commonly occurs in North, Central and Mesoamerica (Santos and Brescovit 2003). While some studies showed that this spider can benefit its host plant by removing phytophagous insects (Arango et al. 2000; Louda 1982), others considered it as a good biological control agent in North American agroecosystems (Nyffeler et al. 1987, 1992a, 1992b).

In southeastern Brazil, *Peucetia flava* Keyserling 1877 (Oxyopidae) occurs frequently associated with *Rhynchanthera dichotoma* (Lam.) DC. (Melastomataceae), a glandular shrubby plant that typically inhabits swamps. To better understand the *Peucetia*–*Rhynchanthera* system, we (1) described the population fluctuation and phenology of *Peucetia*; (2) evaluated if the seasonal density fluctuation of this spider species is determined

by seasonality of biotic and/or abiotic factors (e.g., rainfall, abundance of leaves and arthropods) and, (3) determined the sex ratio of this spider population over the study.

Material and methods

Study area and organisms

This work was done in a swamp site along an affluent margin of a lake (altitude 494 m; 20°49'S, 49°20'W) in São José do Rio Preto city, northwest of the state of São Paulo, southeastern Brazil. The climate of the study area is seasonal, with a mean monthly temperature varying from 21°C in July to 28°C in September. The driest periods during this study were from April to August, with a mean monthly pluviosity varying from 0 mm in July to 323.7 mm in January (see Figure 1B).

Rhynchanthera dichotoma is a hydrophitic phanerogamic shrub (0.5-2.0 m high) that occurs in temporary aquatic ecosystems (i.e., swamps). This plant is frequently a habitat for various arthropod guilds, including phytophages (e.g., Curculionidae, Miridae, Aphididae, Homoptera) and predators (e.g., spiders, Reduviidae). Furthermore, many insects (e.g., ants, Chironomidae, Aphididae) are eventually adhered to the glandular trichomes, which are very dense in leaves and young stems on this plant species (J. C. Morais-Filho and G. Q. Romero, personal observations). The spider *Peucetia flava* is the most common predator on this plant species, and uses the plants as foraging and reproductive sites; it preys on chewers, suckers, pollinators, predators and arthropods adhered to the glandular trichomes (J. C. Morais-Filho and G. Q. Romero, personal observations).

Seasonal density fluctuation

The seasonal density fluctuation of *Peucetia* was assessed between December 2005 and December 2006 by monthly inspections of 16-32 *Rhynchanthera* plants that were previously marked in a 20x40 m open area. This variation in the number of *Rhynchanthera* plants occurred because during the study some plants were severely damaged by cattle. Each plant was surveyed during 5-10 min, according to the plant size. For each individual of *Peucetia* found, we measured its body length using a paquimeter scale over the spider and recorded its sex. The number of egg sacs was also recorded. After surveys, we recorded the height, number of branches, leaves, flowers, fruits, as well as total number of insects on each plant. The seasonal fluctuation was determined by the spider density over the study. The spider density was calculated as the number of spiders divided by the number of branches; the product was multiplied by the mean number of branches per plant (i.e., 180 branches) to

obtain an estimate of the actual spider population size. The phenology was represented by the temporal variation (in months) in spider age structure, according to Romero and Vasconcellos-Neto (2003). To determine the age structure, we used spider size to infer about its age: spiders having total body length (cephalothorax + abdomen) of ≤ 3.0 mm were classified as young, > 3.0 mm but ≤ 6.0 mm as juveniles, > 6.0 mm as subadult + adult females (without dilated palps and beige to red abdomen), > 6.0 mm but ≤ 7.0 mm as the subadult males (with a dilated palp and slightly orange abdomen), and > 7.0 mm as adult males (with a dilated sclerotized palp and orange abdomen).

Synchrony and displacement among events

Multiple linear regression analysis (Zar 1996) with up to three months of temporal displacement was used to assess what biotic and abiotic factors affected the seasonal density fluctuation of *Peucetia*. For each analysis the dependent variables were the density (number per 180 branches per month) of all spiders, as well as density of adults, subadults, juveniles, young and egg sacs; the independent variables were rainfall, temperature and density (number per 180 branches per month) of leaves, flowers, fruits, as well as free and adhered arthropods to glandular trichomes. All variables were obtained monthly and the delay was applied only to the dependent variables, following Arango et al. (2000) and Romero and Vasconcellos-Neto (2003). Prior to the analyses, the data were log or log (n+1) transformed to obtain normally distributed frequency distributions and equalization of variances.

The effects of biotic and abiotic factors were also tested for the density (number per 180 branches per month) of free and adhered arthropods (dependent variables), in which rainfall, leaves and flowers were the independent variables chosen as above. The effects of abiotic factors (i.e., rainfall and temperature) were tested for the density (number per 180 branches) of leaves, flowers and fruits (dependent variables) of *Rhynchanthera*. Temperature and rainfall data were obtained from the “Escritório de Desenvolvimento Rural (EDR)” which has a meteorological station ca. 7 km apart from the study area.

Sex ratio

The sex ratio of *Peucetia* was monitored monthly throughout the study and was calculated for subadult + adult males versus subadult + adult females. The sex ratio of *Peucetia* was tested for a statistically significant difference from 1:1 using G-test (Zar 1996).

Results

Seasonal density fluctuation

Peucetia flava occurred on *Rhynchanthera dichotoma* throughout the year during the observation and the size of this spider population varied few over time (Figure 1A). Similarly, the abundance of leaves also varied few over time (Figure 1A). The population size of *Peucetia* reached the highest density in February and the lowest density in the cold/dry season (April-August), corresponding to the flowering period of *Rhynchanthera* (Figure 1A, B). The number of flowers reached a peak in April and subsequently the number of fruits reached a peak in June (Figure 1A). The number of arthropods (i.e., total, free and adhered arthropods) varied throughout the year, with the highest density (October-February) corresponding to the hot/rainy season and the lowest density (March-September) corresponding to the cold/dry season (Figure 1B, C). In May the density of arthropods (i.e., spiders, egg sacs, total, free and adhered arthropods) were extremely reduced and returned to increase in June, in the dry season (Figure 1A, B, C).

Peucetia produced egg sacs throughout the year, except in May, September and November (Figure 1A). Young recruitment occurred in all months with prominent peaks in February and October (Figure 2). The proportion of juveniles started to increase in October and reached a peak in December 2006 (Figure 2). Young and juveniles together represented the majority of the individuals (51%–88%) in the *Peucetia* population, except in June and July (50% and 46%, respectively). Subadult and adult males did not occur throughout the year and the highest proportions were reached in July for subadults and September for adults (Figure 2). Subadult females reached a peak in May and adult females in August (Figure 2).

Synchrony and displacement between events

The multiple linear regression test concerning all the seven independent variables detected multicollinearity. We then removed some independent variables following procedures suggested by Zar (1996): we first run a linear regression analysis between all independent variables and selected those with the smallest r^2 value (i.e., rainfall, number of leaves, free arthropods and adhered arthropods). The test still detected multicollinearity, so we did a second selection of independent variables, following the procedure described above, and excluded the free arthropod variable remaining only three variables that better adjusted to the model (i.e., rainfall, leaves and adhered arthropods). The density of *Peucetia* individuals (total number) and of the young correlated positively with the abundance of leaves and, with one month of displacement, to adhered arthropods (potential prey) (Table I). However, these

variables were not correlated to rainfall. Adults, subadults, juveniles and egg sacs did not correlate with any independent variables (Table I).

Free and adhered arthropods correlated positively with all the independent variables (Table II). They correlated positively with rainfall, but 3 months after the beginning of this independent variable. The number of free arthropods increased 2-3 months after increase in leaf production and 1-3 months after flower production. The number of adhered arthropods increased 1 and 3 months after increase in leaf production and responded positively to flower production in all months (Table II). The response of leaf, flower and fruit abundances occurred only three months after the beginning of the rainfall (leaves: $t = 3.145$, $P = 0.016$; flowers: $t = 3.287$, $P = 0.013$; fruits: $t = 3.258$, $P = 0.014$). Temperature did not influence these dependent variables ($0.493 > P > 0.058$).

Sex ratio

Females were more frequent compared to males, and this occurred throughout the year. Statistical difference was observed between December 2005 and June 2006 (Table III).

Discussion

Our findings indicate that the life cycle of *P. flava* is non-seasonal, i.e., the population size varied few over the year. Consequently, mating, production of egg sacs, hatching, dispersal and growth of the young occurred concomitantly over the year independently of the seasonality of abiotic factors (e.g., rainfall). The stability of the population fluctuation of *P. flava* over the year is unusual if compared to those already described for several other spiders (e.g., Romero and Vasconcellos-Neto 2003), including other *Peucetia* species (Brady 1964; Whitcomb et al. 1966; Arango et al. 2000). For instance, in USA and Mexico the populations of *Peucetia viridans* presented a life cycle synchronized with the physical changes in the environment (Brady 1964; Whitcomb et al. 1966; Arango et al. 2000). In USA, the life cycle of *P. viridans* were reported to start with mating in the dry season (July), eggs are laid at the beginning of the rainy season (September), hatching and dispersal during rainfall (November to January), and growth until the dry season (January to June) (Brady 1964; Whitcomb et al. 1966). In addition, in Mexico the abundance of *P. viridans* increases when precipitation increases and the life cycle of this spider species is similar to those described for USA, although displaced two months due to differences in the climatic patterns, indicating that the phenology of *P. viridans* is closely related to the changes of the physical environment (Arango et al. 2000).

The unusual stability of the population fluctuation of *P. flava* over the year may be explained by the proximity of the *Rhynchanthera* shrubs to a water source (stream). This may have provisioned the spider population with allochthonous resources (i.e., aquatic insects that migrate to terrestrial environments), which thus buffered population fluctuations. Similar results were also obtained by Romero and Vasconcellos-Neto (2005c), which reported low amplitude of variation of *Psecas chapoda* (Salticidae) population on *Bromelia balansae* (Bromeliaceae) during the year; in addition, like *P. flava*, females of this salticid species has no seasonal period of reproduction and produce egg sacs all over the year. In fact, both populations of *Ps. chapoda* and *P. flava* are under a similar environmental influence, i.e., the proximity from a water source. Recent studies reported that several spider families are more abundant where aquatic insects occur abundantly (e.g., Marczak and Richardson 2007). Therefore, the stability in the seasonal fluctuations of *P. flava* may be related to the type of habitat that this spider occurs (swamp).

Our multiple regression analyses showed that after three months of the beginning of the rainfall *Rhynchanthera* started to increase the production of vegetative and reproductive branches. The number of arthropods responded to rainfall concomitantly with *Rhynchanthera* and also responded to the increase in abundance of vegetative and reproductive branches. Finally, the number of spiders (total and young) responded positively to the increase in abundance of leaves, which bear glandular trichomes, as well as to the increase in number of arthropods adhered to these sticky structures. Several spiders of the genus *Peucetia* were reported to live on plants with glandular trichomes and these associations likely evolved because these structures may facilitate prey capture for the spiders (Romero and Vasconcellos-Neto 2003; Vasconcellos-Neto et al. 2007). Thus, glandular trichomes seem not only to mediate spider-plant associations (Vasconcellos-Neto et al. 2007), but also influence on spider seasonal density fluctuation.

Throughout the year females were more frequent relative to males. This likely occurred because males migrate between plants more than females (J. C. Morais-Filho, personal observation). Outside the plants males probably are more vulnerable to predators. Thus, males may have been more preyed on by natural enemies than females, resulting in populations with more females than males. Similar results were obtained by Romero and Vasconcellos-Neto (2005c).

In conclusion, these results indicated that bottom-up forces may influence this spider-plant system, since our multiple regression analyses showed a correlation between the seasonal density fluctuation of *Peucetia flava* and the increase in abundance of leaves and

food source (i.e., adhered arthropods). In addition, the constant input of allochthonous resources seems to supply the constant young recruitment that maintained the population size stable. Females were more frequent than males, and this probably occurred because males are more vulnerable to predation than females. This study is a first approach toward comprehension of this spider-plant system and further investigations on the strength of top-down forces caused by *Peucetia flava* could help evaluate the dynamics of this spider-plant system.

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Table I. The coefficient (and *P* values in parenthesis) of multiple linear regression analyses examining the effects of rainfall, abundance of leaves and number of adhered arthropods on the density of individuals of *Peucetia flava*, displaced 1, 2 and 3 months relative to the dependent variable (spider density). Significant *P* values are in boldface.

Spiders	Displacement (in months)	Rainfall (mm)	Leaves	Adhered arthropods
Total	0	0.301 (0.770)	4.545 (0.001)	0.492 (0.634)
	1	1.778 (0.113)	0.511 (0.623)	2.988 (0.017)
	2	1.039 (0.333)	1.003 (0.349)	2.041 (0.081)
	3	1.315 (0.237)	0.110 (0.916)	1.119 (0.306)
Adults	0	0.918 (0.383)	2.062 (0.069)	1.123 (0.290)
	1	0.197 (0.848)	0.007 (0.994)	0.196 (0.850)
	2	0.159 (0.878)	0.083 (0.936)	0.541 (0.606)
	3	0.104 (0.921)	0.160 (0.878)	0.453 (0.666)
Subadults	0	0.740 (0.478)	0.617 (0.553)	0.481 (0.642)
	1	0.137 (0.894)	0.144 (0.889)	1.525 (0.166)
	2	1.016 (0.343)	0.144 (0.889)	1.644 (0.144)
	3	0.890 (0.408)	0.300 (0.774)	0.340 (0.745)
Juveniles	0	0.868 (0.408)	0.754 (0.470)	0.670 (0.520)
	1	0.600 (0.565)	0.652 (0.533)	0.786 (0.455)
	2	1.114 (0.302)	0.043 (0.966)	1.181 (0.276)
	3	1.548 (0.173)	1.131 (0.301)	1.008 (0.352)
Young	0	0.141 (0.891)	3.914 (0.004)	0.841 (0.422)
	1	1.282 (0.236)	1.201 (0.264)	2.994 (0.017)
	2	0.638 (0.544)	1.204 (0.268)	1.671 (0.139)
	3	2.355 (0.057)	1.024 (0.345)	0.097 (0.926)
Egg sacs	0	1.277 (0.234)	1.569 (0.151)	0.076 (0.941)
	1	0.409 (0.693)	0.036 (0.972)	0.424 (0.683)
	2	0.366 (0.725)	0.188 (0.856)	0.280 (0.787)
	3	0.562 (0.594)	0.813 (0.448)	0.194 (0.852)

Table II. The coefficient (and *P* values in parenthesis) of multiple linear regression analyses examining the effects of rainfall, abundance of leaves and flowers on the density of free and adhered arthropods, displaced 1, 2 and 3 months relative to the dependent variable (arthropod density). Significant *P* values are in boldface.

Arthropods	Delay	Rainfall	Leaves	Flowers
Free	0	1.789 (0.107)	1.450 (0.181)	2.246 (0.051)
	1	0.522 (0.616)	1.657 (0.136)	7.217 (< 0.001)
	2	1.539 (0.168)	2.762 (0.028)	5.608 (< 0.001)
	3	3.909 (0.008)	4.086 (0.006)	5.149 (0.002)
Adhered	0	0.284 (0.783)	0.670 (0.520)	3.425 (0.008)
	1	1.339 (0.217)	6.362 (< 0.001)	12.431 (< 0.001)
	2	2.174 (0.066)	2.068 (0.077)	3.603 (0.009)
	3	3.997 (0.007)	2.690 (0.036)	2.470 (0.048)

Table III. Sex ratios of subadult + adult males versus subadult + adult females of *Peuceitia flava*. Significant *P* values are in boldface.

Month	Males (N)	Females (N)	Sex ratio (M:F)	<i>G</i> -test	<i>P</i>
December	4	22	1:5.50	12.09	< 0.001
January	4	19	1:4.75	9.15	0.002
February	1	19	1:19.00	17.07	< 0.001
March	4	17	1:4.25	7.29	0.007
April	2	11	1:5.50	5.29	0.021
May	1	14	1:14.00	11.04	< 0.001
June	0	16	0:16.00	17.73	< 0.001
July	6	10	1:1.66	0.57	0.452
August	3	11	1:3.66	3.66	0.056
September	3	8	1:2.66	1.49	0.222
October	4	6	1:1.5	0.10	0.752
November	3	2	1:0.66	0.00	1.000
December	3	2	1:0.66	0.00	1.000

The *G*-tests were calculated using Yate's correction.

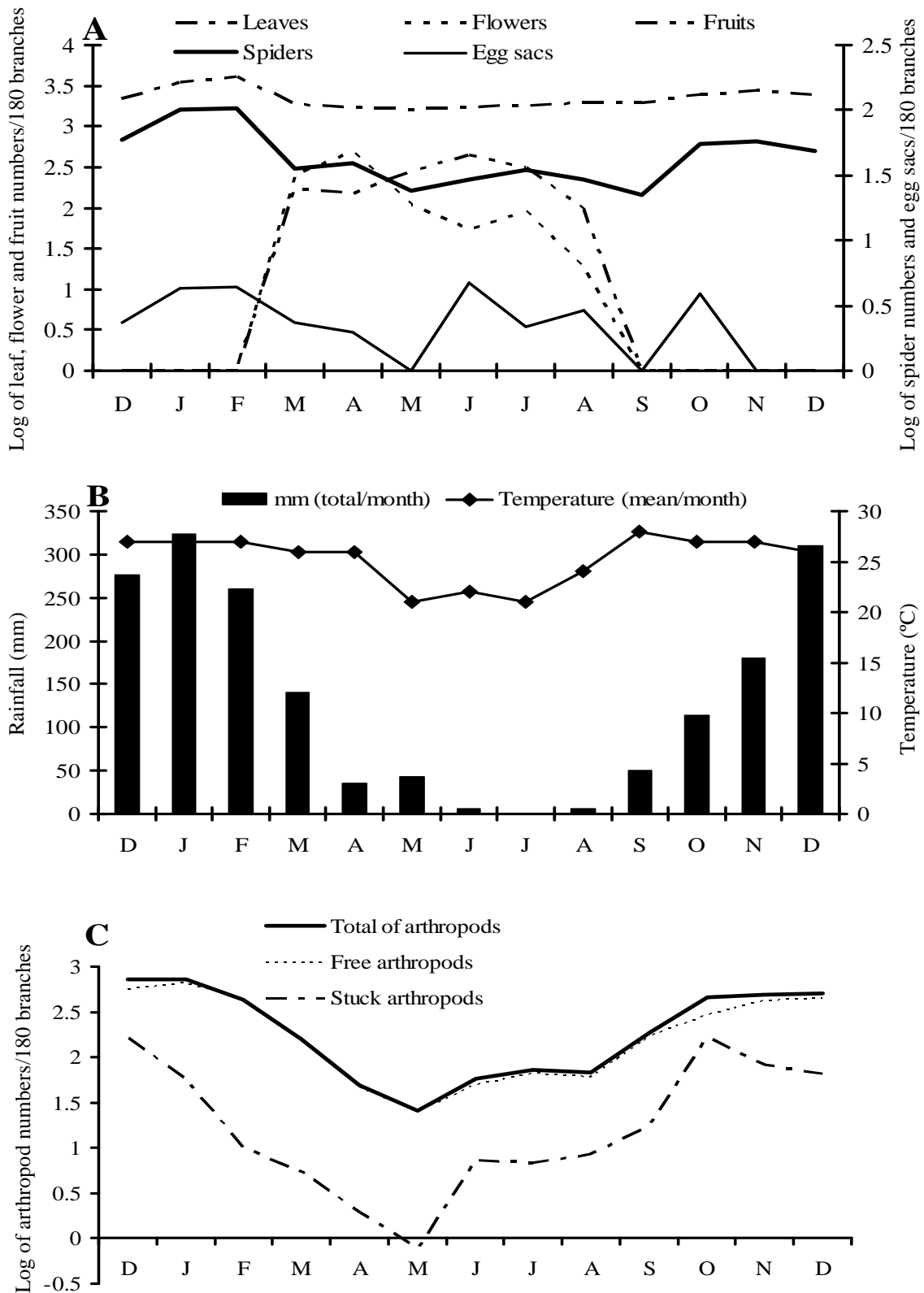


Figure 1. (A) Seasonal fluctuations in the number of *Peucea flava* individuals, egg sacs, abundance of leaves, flowers and fruits of *Rhynchanthera dichotoma*; (B) monthly rainfall and temperature variation during the study period (data from a meteorological station ca. 7 Km apart from the study site); and (C) seasonal fluctuations in the number of free and stuck arthropods at glandular trichomes on leaves of *R. dichotoma*.

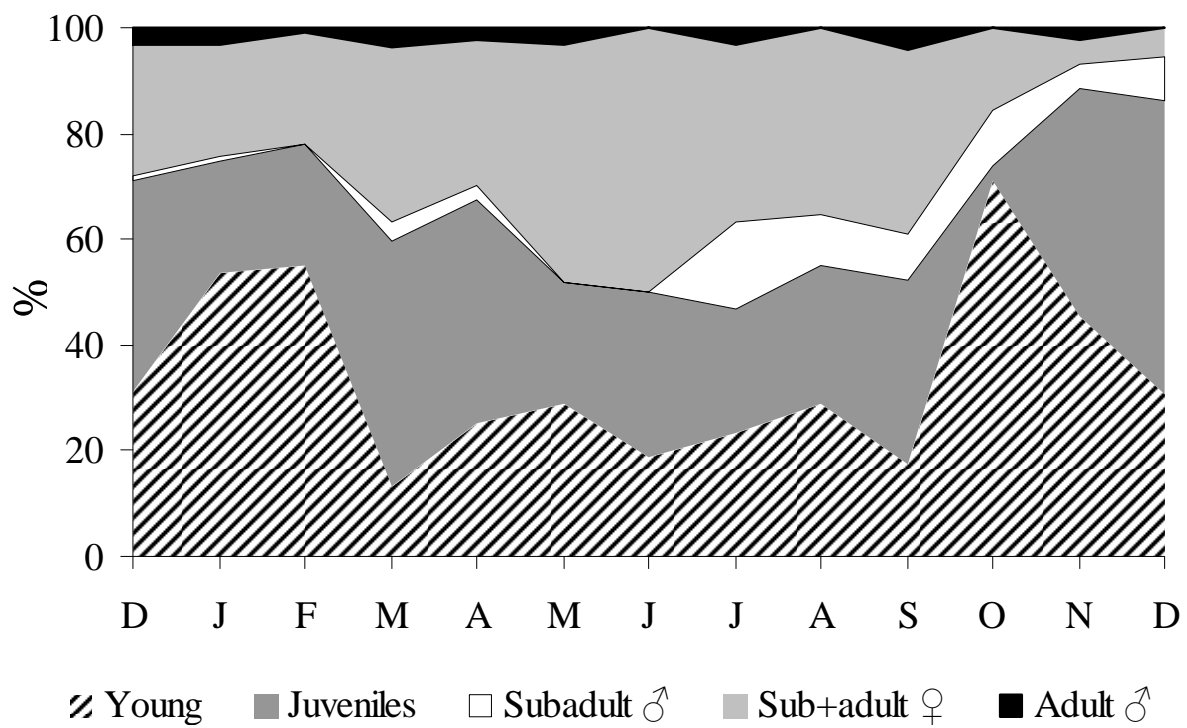


Figure 2. Phenogram of the *Peucetia flava* population on plants of *Rhynchanthera dichotoma*.

5. SÍNTESE

1. Uso de Microhabitat e História Natural

Este estudo demonstra que aranhas *Peucetia flava* na região de São José do Rio Preto ocorrem estritamente sobre a planta com tricomas glandulares *Rhynchantera dichotoma*, onde forrageiam e se reproduzem durante o ano todo. A distribuição espacial destas aranhas foi fortemente influenciada pela altura da planta, número de folhas e número de artrópodes aderidos aos tricomas glandulares. O tamanho populacional de *P. flava* foi fortemente influenciado pelo aumento na abundância de folhas e de artrópodes aderidos aos tricomas glandulares, indicando que plantas com maior número de folhas representam melhores sítios de forrageamento e proteção. O tamanho populacional de *P. flava* oscilou pouco ao longo do ano. Esta estabilidade incomum observada na flutuação populacional destas aranhas pode ser explicada pela proximidade de *R. dichotoma* a um curso d'água, o qual pode ter provido esta população com recursos alóctones: insetos aquáticos (e.g., Chironomidae) que migram para o meio terrestre e ficam aderidos aos tricomas glandulares. Concluímos que esta associação ocorre devido à presença de tricomas glandulares que beneficiam aranhas por facilitarem a captura de artrópodes. Nesta planta, as aranhas avaliam diferentes parâmetros ao longo do ano, sendo afetadas principalmente pela abundância de folhas. Ocorrendo em plantas com maior número de folhas, as aranhas aumentam a chance de se alimentarem de presas aderidas aos tricomas glandulares ou até mesmo de carcaças, podendo atuar como carniceiras nos períodos de escassez de presas. Além disso, a constante entrada de recursos alóctones provenientes do meio aquático mantém a população estável pelo suprimento do constante recrutamento de jovens.

2. Mutualismo

A associação entre *P. flava* e *R. dichotoma* se caracteriza como uma associação íntima e persistente ao longo do tempo, em que a presença de tricomas glandulares media um mutualismo facultativo. Estas aranhas apresentam efeito táxon-específico sobre os artrópodes presentes sobre estas plantas. Neste sistema as aranhas reduzem significativamente as taxas de herbivoria floral e foliar, entretanto neste último, seus efeitos como guarda-costas são condicionados temporalmente em razão de efeitos *bottom-up* (i.e., incremento em biomassa vegetativa) que mascaram os efeitos predatórios das aranhas e a redução das taxas de herbivoria foliar no período chuvoso. Além disso, a presença das aranhas reduz o número de botões inviáveis sem afetar o número de sementes produzidas por planta, indicando que a presença das aranhas é somente benéfica para as plantas. Esta especialização de *P. flava* sobre

R. dichotoma possivelmente se deve a função análoga dos tricomas glandulares a uma teia de aranha que facilita a captura de presas, reduzindo o gasto energético das aranhas. Estas aranhas selecionam plantas com tricomas glandulares, permanecendo mais tempo sobre elas do que em plantas com tricomas glandulares removidos. Além disso, análises isotópicas demonstram que estas aranhas se alimentaram de presas vivas e mortas presas aos tricomas glandulares, indicando que estas aranhas podem atuar como carniceiras neste sistema mutualístico.