unesp

CAMPUS DE SÃO JOSÉ DO RIO PRETO

SELEÇÃO DE PLANTAS HOSPEDEIRAS PELA ARANHA BROMELÍCOLA *PSECAS CHAPODA* (SALTICIDAE)

Paula Munhoz de Omena

MESTRADO

PÓS GRADUAÇÃO EM BIOLOGIA ANIMAL

2009

UNIVERSIDADE ESTADUAL PAULISTA

INSTITUTO DE BIOCIÊNCIAS, LETRAS E CIÊNCIAS EXATAS

SÃO JOSÉ DO RIO PRETO – SP

PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA ANIMAL

PAULA MUNHOZ DE OMENA

SELEÇÃO DE PLANTAS HOSPEDEIRAS PELA ARANHA BROMELÍCOLA *PSECAS CHAPODA* (SALTICIDAE)

Dissertação apresentada ao Instituto de Biociências, Letras e Ciências Exatas, Universidade Estadual Paulista, para obtenção do título de mestre em Biologia Animal.

ORIENTADOR: DR. GUSTAVO QUEVEDO ROMERO

- 2009 –

Data da defesa: 27 de abril de 2009

BANCA EXAMINADORA

TITULARES:

DR. GUSTAVO QUEVEDO ROMERO (ORIENTADOR)   _____

UNESP/São José do Rio Preto – SP

PROF. DR. MARCELO DE OLIVEIRA GONZAGA   _____

UNIVERSIDADE FEDERAL DE UBERLÂNDIA – MG

DR. PAULO ENRIQUE CARDOSO PEIXOTO   _____

UNIVERSIDADE ESTADUAL DE CAMPINAS – SP

SUPLENTES:

PROF. DR. JOÃO VASCONCELLOS-NETO   _____

UNIVERSIDADE ESTADUAL DE CAMPINAS – SP

PROFA. DRA. LILIAN CASATTI   _____

UNESP/São José do Rio Preto – SP

AGRADECIMENTOS

DEDICO ESTE TRABALHO
AOS MEUS PAIS DJALMA E SONIA
E À MINHA IRMÃ LUCIANE,
COM TODO MEU AMOR.

SUMÁRIO

RESUMO

A aranha *Psecas chapoda* (Salticidae) utiliza a planta *Bromelia balansae* (Bromeliaceae) como sítio de forrageamento, acasalamento e postura de ootecas, bem como abrigo contra predadores e berçário. Em contraste com outras espécies de salticídeos bromelícolas, que habitam até 7-8 espécies de bromélias em regiões litorâneas, *P. chapoda* habita quase exclusivamente *B. balansae* em regiões de Cerrado e margens de Florestas Semidecíduas. Esta especialização possivelmente ocorre porque as áreas de vida de *P. chapoda* são dominadas apenas por *B. balansae*, não havendo bromélias de outras espécies/arquiteturas disponíveis para as aranhas. Neste trabalho realizamos experimentos com os objetivos de: (1) testar se a associação de *P. chapoda* restringia-se a uma planta hospedeira específica ou a plantas com um tipo específico de arquitetura; (2) verificar se indivíduos adultos de *P. cha*poda escolhiam ativamente suas plantas hospedeiras e (3) determinar os mecanismos sensoriais envolvidos na seleção de plantas hospedeiras por *P. chapoda*. Nossos resultados mostraram que a especialização deste salticídeo por micro-hábitat não é espécie-específica e sim restrita a certas características arquiteturais das rosetas de suas plantas hospedeiras. *Psecas chapoda*, guiada por estímulos visuais, avalia e distingue estruturas físicas de micro-hábitats e seleciona ativamente plantas em roseta com folhas longas e estreitas. Este padrão é incomum entre predadores invertebrados, e, provavelmente, evoluiu em virtude da grande abundância de um tipo específico de micro-hábitat aliado a excelente acuidade visual de *P. chapoda* que possibilita a detecção eficiente de suas plantas hospedeiras.

1. Introdução Geral

Aranhas e estrutura da vegetação

As aranhas estão entre os animais mais abundantes nos ambientes terrestres, existindo 40.700 espécies descritas (Coddington & Levi, 1991; Platnick, 2009). Ocupam os mais diversos hábitats e, embora estejam entre os artrópodes mais abundantes sobre a vegetação, suas inter-relações com as plantas são ainda relativamente pouco conhecidas (Romero, 2006). Organismos tipicamente predadores, as aranhas interagem de maneira indireta com a vegetação, com exceção das espécies que utilizam pólen e néctar como fonte alternativa de alimento (revisão em Romero & Vasconcellos-Neto, 2007).

A distribuição espacial e a abundância das aranhas que vivem na vegetação são fortemente modeladas por variações arquiteturais das plantas e do hábitat (Colebourn 1974; Greenquist & Rovner, 1976, Robinson 1981; Gunnarsson 1990, 1992, Woodcock *et al*., 2007). Por exemplo, Gunnarsson (1990) demonstrou experimentalmente que a abundância de aranhas é reduzida com a diminuição do número de folhas nos ramos de *Picea abies* (Pinaceae). Mudanças na arquitetura da bromélia *Bromelia balansae* (Bromeliaceae) durante o período de floração tornam a colonização pela aranha *Psecas chapoda* (Salticidae) menos favorável. Durante a floração a disposição das folhas de *B. balansae* muda de uma configuração cônica tridimensional para uma configuração plana quase bidimensional (Figura 1 A e B). Tal alteração modifica as áreas de abrigo (i.e., centro da roseta, que é ocupado pela inflorescência), bem como sítios de forrageamento, acasalamento, oviposição e berçário (Romero & Vasconcellos-Neto, 2005a). Por meio de um estudo meta-analítico, Langellotto & Denno (2004) demonstraram que vários táxons de artrópodes terrestres respondiam positivamente ao aumento da complexidade estrutural do hábitat e negativamente à sua simplificação. Notavelmente, as aranhas

cursoriais foram os artrópodes que apresentaram os maiores aumentos em abundância com o incremento da complexidade estrutural; enquanto a diminuição da complexidade afetava principalmente as aranhas construtoras de teias (Langellotto & Denno, 2004).

Experimentos com vegetação artificial e natural mostraram que diferentes grupos e guildas de aranhas preferem diferentes tipos de arquitetura (Robinson, 1981; Wise, 1993). Estes organismos são hábeis em escolher os melhores micro-hábitats para forrageamento (Morse & Fritz, 1982; Morse, 1990; Romero & Vasconcellos-Neto, 2004a, b, 2005a, b), cópula, oviposição (Rossa-Feres *et al*., 2000; Smith, 2000; Figueira & Vasconcellos-Neto, 1993; Romero & Vasconcellos-Neto, 2005 b, c) e abrigo (Gunnarsson 1990, 1996; Romero & Vasconcellos-Neto, 2005a). Por exemplo, a aranha *Misumena vatia* (Thomisidae) seleciona ativamente sítios mais ricos em presas (e.g., ramos reprodutivos) (revisão em Morse, 2007) e prefere a planta *Asclepias*, dentre várias outras espécies, como sítio de oviposição (Morse, 1990). Esta seleção provavelmente ocorre porque as folhas desta planta são maiores, mais flexíveis e apresentam alta densidade de tricomas foliares, que protegem os ovos contra parasitóides. Neste caso, a escolha do micro-hábitat para oviposição está mais relacionada à pressão do predador sobre a prole do que com a qualidade de alimento disponível.

Associações específicas

Apesar das aranhas geralmente não manterem associações específicas com plantas, estudos recentes demonstraram que algumas espécies das famílias Oxyopidae, Thomisidae, Salticidae e uma espécie de Araneidae vivem estritamente associadas a espécies específicas de plantas ou a grupos de plantas que partilham características

morfológicas em comum (e.g., plantas com tricomas glandulares ou com arquitetura em rosetas) (Romero, 2005; Romero, 2006; Romero & Vasconcellos-Neto, 2007). Várias espécies do gênero *Peucetia* (Oxyopidae) foram encontradas associadas a plantas com tricomas glandulares em diversas localidades nas regiões Neotropical, Neartica, Paleartica e Afrotropical (Vasconcellos-Neto *et al*., 2007). Estes organismos podem ter se adaptado a viver sobre plantas com tais tricomas uma vez que, insetos aderidos a estas estruturas adesivas, podem ser utilizados como presas pelas aranhas (Romero & Vasconcellos-Neto, 2003, 2004a, b; Vasconcellos-Neto *et al.*, 2007). A aranha *Alpaida quadrilorata* (Araneidae) habita quase exclusivamente *Paepalanthus bromelioides* (Eriocaulaceae), uma planta semelhante à Bromeliaceae. Estas plantas possuem arquitetura em roseta que fornece substrato para forrageamento, abrigo e proteção (Figueira & Vasconcellos-Neto, 1991). Várias espécies de aranhas da família Salticidae são também encontradas associadas à Bromeliaceae (e.g., Romero, 2006).

As plantas da família Bromeliaceae podem constituir um micro-hábitat favorável para a sobrevivência de várias espécies de artrópodes (Diesel, 1992a, b; Romero & Vasconcellos-Neto, 2005a, c; Romero, 2006). Suas folhas são planas e formam uma estrutura aberta com uma complexa arquitetura tridimensional, que fornece abrigo e área de forrageamento para diversos grupos animais. Em regiões neotropicais, associações entre aranhas e Bromeliaceae são especialmente comuns (Barth *et al.*, 1988a, b; Santos *et al.*, 2002; Dias & Brescovit, 2003, 2004; Romero & Vasconcellos-Neto, 2004c, 2005a, b, c; Romero *et al.*, 2006; Romero, 2006). Por exemplo, as aranhas *Pachistopelma rufonigrum* (Theraphosidae) e *Nothroctenus fuxico* (Ctenidae) habitam bromélias-tanque no nordeste do Brasil e, aparentemente, utilizam esta planta como área de proteção contra as elevadas temperaturas do solo arenoso (Santos *et al.*, 2002; Dias

5

& Brescovit, 2003, 2004). Estudos recentes mostraram que nove espécies de Salticidae vivem associadas à Bromeliaceae (Rossa-Feres *et al*., 2000; Romero &Vasconcellos-Neto, 2004c, 2005a, b, c; Romero, 2006) em diversos tipos de vegetações em várias regiões do Brasil, Bolívia, Argentina e Paraguai (Romero, 2006).

Seleção de plantas hospedeiras

Aranhas podem selecionar substratos com base em estímulos visuais (Greco & Kevan, 1994; Heiling *et al*., 2005), táteis (Morse, 1988; Greco & Kevan, 1994) e químicos (Aldrich & Barros, 1995; Krell & Krämer, 1998; Heiling *et al*., 2004). Aranhas da família Thomisidae, por exemplo, são atraídas por fragrâncias florais (i.e., eugenol) (Aldrich & Barros, 1995; Krell & Krämer, 1998) e também utilizam características visuais e táteis para selecionarem os melhores locais para forrageamento (Greco & Kevan, 1994; Morse, 1988). Greco & Kevan (1994) encontraram que fêmeas de *Misumena vatia* (Thomisidae), em arenas experimentais, escolhiam preferencialmente ramos com flores intactas a ramos com flores senescentes e, preferiam flores amarelas a outras cores oferecidas. Ainda, Heiling *et al*. (2005) verificaram experimentalmente que, aranhas *Thomisus spectabilis* (Thomisidae) selecionavam sítios de forrageamento de acordo com a sua própria coloração corporal. Quando oferecidas flores amarelas e brancas (i.e., *Chrysanthemum frutescens*) *T. spectabilis* amarelos escolhiam apenas flores amarelas.

Embora vários estudos tenham descrito associações específicas entre aranhas e plantas, poucos determinaram os mecanismos envolvidos na seleção de plantas hospedeiras por aranhas. Dentre as aranhas bromelícolas, apenas um estudo demonstrou, por meio de experimentos em campo, os efeitos de modificações

arquiteturais de plantas (i.e., *B. balansae*) na sua colonização por aranhas (i.e., *P. chapoda*) (Romero & Vasconcellos-Neto, 2005a). Estudos experimentais que investigam como aranhas especialistas de micro-hábitats selecionam suas plantas hospedeiras são tão importantes quanto os que testam quais sítios de forrageamento são escolhidos por aranhas não especialistas. Aranhas especialistas, além de usarem suas plantas hospedeiras como sítios de forrageamento, dependem exclusivamente destas para completarem seus ciclos de vida. Estudos experimentais que testam escolha de plantas específicas por aranhas são inéditos e têm grande importância para a compreensão dos fatores levaram à especialização e evolução de aranhas em arquiteturas específicas de plantas.

Sistema de Estudo

A aranha saltadora *Psecas chapoda* (Peckham & Peckham, 1984) (Salticidae) vive quase exclusivamente associada à planta *Bromelia balansae* Mez. (Bromeliaceae) em uma grande extensão geográfica, abrangendo Paraguai, Bolívia e quatro estados brasileiros: Mato Grosso (MT), Mato Grosso do Sul (MS), São Paulo (SP) e Rio Grande do Sul (RS) (Romero, 2006). Estudos recentes mostraram que o ciclo de vida completo desta aranha incluindo: comportamento de corte, acasalamento, construção de ootecas e recrutamento populacional dos jovens, ocorre sobre a planta *B. balansae* (Rossa-Feres *et al.*, 2000; Romero & Vasconcellos-Neto, 2005a, b). *Bromelia balansae* é provavelmente um excelente micro-hábitat para a reprodução e sobrevivência tanto dos imaturos quanto dos adultos (Romero & Vasconcellos-Neto, 2005a, b, c). Durante o comportamento de corte os machos (Figura 1C) ocupam a região superior das folhas enquanto as fêmeas (Figura 1D) tendem a permanecer próximas a base da roseta

(Rossa-Feres *et al*., 2000). De uma a três ootecas são produzidas e depositadas na região mediana e na superfície côncava das folhas, em cujas margens ancoram-se uma tela plana de seda. As fêmeas permanecem entre a tela plana e a ootecas até os imaturos emergirem (Figura 2A) (Rossa-Feres *et al*., 2000; Romero & Vasconcellos-Neto, 2005c). Vieira & Romero (2008) demonstraram experimentalmente que a presença das fêmeas sobre as ootecas favorece a sobrevivência dos imaturos. Ainda, os autores verificaram que a construção das ootecas é realizada principalmente nas folhas centrais da roseta. Isto possibilita que os imaturos, após emergirem, encontrem seu abrigo (i.e., centro da roseta) mais rapidamente, tornando-os menos expostos à dessecação e ao canibalismo (Romero & Vasconcellos-Neto, 2005a). Os adultos e jovens de diferentes idades utilizam a base da roseta como área de proteção (Figura 2B); quando um observador aproxima-se das bromélias, os indivíduos fogem rapidamente para a base da roseta, escondendo-se de possíveis ataques. Tal estrutura do micro-hábitat serve tanto como área de refúgio e proteção contra dessecação, como para local de descanso (Romero & Vasconcellos-Neto, 2005b). Não somente, *B. balansae* provê as populações de *P. chapoda* proteção contra o fogo (Foto 2C e D) (Omena & Romero, dados não publicados), sendo este um elemento extremamente comum do cerrado, tal proteção pode ter favorecido o estabelecimento desta aranha neste bioma.

Objetivos Gerais

Esta dissertação teve como objetivos principais: (1) Determinar se a associação de *P. chapoda* à *B. balansae* ocorre em virtude da adaptação da aranha a um tipo específico de arquitetura de planta; (2) Testar se aranhas adultas de *P. chapoda* escolhem ativamente suas plantas hospedeiras e (3) Determinar os mecanismos sensoriais envolvidos na seleção de plantas hospedeiras por *P. chapoda*.

Figura 1: *Bromelia balansae* em estado vegetativo (A), *B. balansae* com inflorescência (B), macho adulto de *Psecas chapoda* (C) e fêmea adulta de *P. chapoda* (D).

Figura 2: Fêmea adulta sobre ooteca (A), fêmea utilizando a base da roseta como área de proteção (B), moita de bromélias após queimada (C) e jovem sobrevivente no centro da roseta de *B. balansae* (D).

LITERATURA CITADA

Aldrich JD, Barros TM. 1995. Chemical attraction of male crab spiders (Araneae, Thomisidae) and Kleptoparasitic flies (Diptera, Milichiidae, and Chloropidae). *Journal of Arachnology* **23:** 212-214.

Barth FG, Seyfarth EA. 1979. *Cupiennius salei* Keyserling (Araneae) in the highlands of central Guatemala. *Journal of Arachnology* **7:** 255-263.

Barth FG, Bleckmann H, Bohnenberger J, Seyfarth EA. 1988a. Spiders of the genus *Cupiennius* Simon 1891 (Araneae, Ctenidae). II. On the vibratory environment of a wandering spider. *Oecologia* **77:**194-201.

Barth FG, Seyfarth EA, Bleckmann H, Schüch W. 1988b. Spiders of the genus *Cupiennius* Simon 1891 (Araneae, Ctenidae). I. Range distribution, dwelling plants, and climatic characteristics of the habitats. *Oecologia* **77:**187-193.

Chien SA, Morse DH. 1998. The role of prey and flower quality in the choice of hunting sites by adult male crab spiders *Misumena vatia* (Araneae, Thomisidae). *Journal of Arachnology* **26:**238-243.

Colebourne PH. 1974. The influence of habitat structure on the distribution of *Araneus diadematus* Clerck. *Journal of Animal Ecology* **43:** 401-409.

Coddington JA, Levi HW. 1991. Systematics and evolution of spiders (Araneae). *Annual Review of Ecology and Systematics* **22:**565-592.

Dias SC, Brescovit AD. 2003. Notes on the behavior of *Pachistopelma rufonigrum* Pocock (Araneae, Theraphosidae, Aviculariinae). *Revista Brasileira de Zoologia* **20:** 13-17.

Dias SC, Brescovit AD. 2004. Microhabitat selection and co-occurrence of *Pachistopelma rufonigrum* Pocock (Araneae; Theraphosidae) and *Nothroctenus*

fuxico sp. nov. (Araneae, Ctenidae) in tank bromeliads from Serra de Itabaiana, Sergipe, Brazil. *Revista Brasileira Zoologia* **21:**789-796.

Diesel R. 1992a. Maternal care in the bromeliad crab, *Metopaulias depressus*: protection of larvae from predation by damselfly nymphs. *Animal Behaviour* **43:**803-812.

Diesel R. 1992b. Managing the offspring environment: brood care in the bromeliad crab, *Metopaulias depressus*. *Behavioral Ecology and Sociobiology* **30:**125-134.

Figueira JEC, Vasconcellos-Neto J. 1993. Reproductive success of *Latrodectus geometricus* (Theridiidae) on *Paepalanthus bromelioides* (Eriocaulaceae): rosette size, microclimate, and prey capture. *Ecotropicos* **5:**1-10.

Gunnarsson B. 1990. Vegetation structure and the abundance and size distribution of spruce-living spiders. *Journal of Animal Ecology* **59:**743-752.

Gunnarsson B. 1992. Fractal dimension of plant and body size distribution in spiders. *Functional Ecology* **6:**636-641.

Gunnarsson B. 1996. Bird predation and vegetation structure affecting spruce-living arthropods in a temperate forest. *Journal of Animal Ecology* **65:**389-397.

Greco CF, Kevan PG. 1994. Contrasting patch choosing by anthophilous ambush predators: vegetation and floral cues for decision by a crab spider (*Misumena vatia*) and males and females of an ambush bug (*Phymata Americana*). *Canadian Journal of Zoology* **72:**1583-1588.

Greenquist EA, Rovner JS. 1976. Lycosid spiders on artificial foliage: stratum choice, orientation preferences, and prey-wrapping. *Psyche* **83:**196-209.

Heiling AM, Cheng K, Herberstein ME. 2004. Exploitation of floral signals by crab spiders (*Thomisus spectabilis*, Thomisidae). *Behavioral Ecology* **2:**321-326.

Heiling AM, Chittka L, Cheng K, Herberstein ME. 2005. Colouration in crab spider: substrate choice and prey attraction. *Journal of Experimental Biology* **208:**1785-1792.

Krell FT, Krämer F. 1998. Chemical attraction of crab spiders (Araneae, Thomisidae) to a flower fragrance component. *Journal of Arachnology* **26:**117-119

Langellotto GA, Denno RF. 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia* **139:**1-10.

Morse DH. 1988. Relationship between crab spider *Misumena vatia* nesting success and earlier patch-choice decisions. *Ecology* **69:**1970-1973.

Morse DH. 1990. Leaf choices of nest-building crab spiders (*Misumena vatia*). *Behavioral Ecology and Sociobiology* **27:**265-267.

Morse DH. 2007. *Predator upon a flower: life history and fitness in a crab spider*. Harvard University Press, Cambridge, UK.

Morse DH, Fritz RS. 1982. Experimental and observational studies of patch choice at different scales by the crab spider *Misumena vatia*. *Ecology* **63:**172-182.

Platnick NI. 2009. The world spider catalog. Version 9.5
http://research.amnh.org/entomology/spiders/catalog/COUNTS.html

Robinson JV. 1981. The effect of architectural variation in habitat on a spider community: an experimental field study. *Ecology* **62:**73–80.

Romero GQ. 2005. *Associações entre aranhas Salticidae e Bromeliaceae: história natural, distribuição espacial e mutualismos*. Tese de doutorado, Universidade Estadual de Campinas, Campinas, São Paulo.

Romero GQ. 2006. Geographic range, habitats and host plants of bromeliad-living jumping spiders (Salticidae). *Biotropica* **38:**522-530.

Romero GG, Vasconcellos-Neto J. 2003. Natural history of *Misumenops argenteus* (Thomisidae): seasonality and diet on *Trichogoniopsis adenantha* (Asteraceae). *Journal of Arachnology* **31:** 297-304.

Romero GQ, Vasconcellos-Neto J. 2004a. Foraging by the flower-dwelling spider, *Misumenops argenteus* (Thomisidae), at high prey density sites. *Journal of Natural History* **38:**1287-1292.

Romero GQ, Vasconcellos-Neto J. 2004b. Beneficial effects of flower-dwelling predators on their host plant. *Ecology* **85:**446-457.

Romero GQ, Vasconcellos-Neto J. 2004c. Spatial distribution patterns of jumping spiders associated with terrestrial bromeliads. *Biotropica* **36:**596-601.

Romero GQ, Vasconcellos-Neto J. 2005a. The effects of plant structure on the spatial and microspatial distribution of a bromeliad-living jumping spider (Salticidae). *Journal of Animal Ecology* **74:**12-21.

Romero GQ, Vasconcellos-Neto J. 2005b. Spatial distribution and microhabitat preference of *Psecas chapoda* (Peckham & Peckham) (Araneae, Salticidae). *Journal of Arachnology* **33:**124-134.

Romero GQ, Vasconcellos-Neto J. 2005c. Population dynamics, age, structure and sex ratio of the bromeliad-dwelling jumping spider, *Psecas chapoda* (Salticidae). *Journal of Natural History* **39:**153-163.

Romero GQ, Vasconcellos-Neto J. 2007. Aranhas sobre plantas: dos comportamentos de forrageamento às associações específicas. In: MO Gonzaga, AJ Santos, HF Japyassú (eds.). *Ecologia e comportamento de aranhas*. Interciência, Rio de Janeiro.

Rossa-Feres D de C, Romero GQ, Gonçalves-de-Freitas E, Feres RJF. 2000. Reproductive behavior and seasonal occurrence of *Psecas viridipurpureus* (Salticidae, Ananeae). *Brazilian Journal of Biology* **60:**221-228.

Santos RL, Almeida MG, Nunes JV. 2002. Notes on the association of *Pachistopelma rufonigrum* Pocock 1901 (Theraphosidae) with phytotelm bromeliads in eastern Rio Grande do Norte State, NE-Brazil. *Journal of the Bromeliad Society* **52:**122-124.

Smith H. 2000. The status and conservation of the fen raft spider (*Dolomedes plantarius*) at Redgrave and Lopham Fen National Nature Reserve, England. *Biological Conservation* **95:**153-164.

Vasconcellos-Neto J, Romero GQ, Santos A, Dippenaar-Schoeman AS. 2007. Associations of spiders of the genus *Peucetia* (Oxyopidae) with plants bearing glandular hairs. *Biotropica* **39:**221-226.

Vieira C, Romero GQ. 2008. Maternal care in a neotropical jumping spider (Salticidae). *Journal of Zoology* **276:**237-241.

Wise DH. 1993. *Spiders in ecological webs*. Cambridge University Press. Cambridge (UK). 328p.

Woodcock BA, Potts SG, Westbury DB, Ramsay AJ, Lambert M, Harris SJ, Brown VK. 2007. The importance of sward architecture complexity in structuring predatory and phytophagous invertebrate assemblages. *Ecological Entomology* **32:**302-311.

Foto: Gustavo C. Piccoli

Fine-scale microhabitat selection in a bromeliad-dwelling jumping spider (Salticidae)

Paula M. de Omena[1] and Gustavo Q. Romero[2]*

1. Pós-graduação em Biologia Animal, Instituto de Biociências, Letras e Ciências Exatas (IBILCE), Universidade Estadual Paulista (UNESP), Rua Cristóvão Colombo 2265, CEP 15054-000, São José do Rio Preto-SP, Brazil.

2. Departamento de Zoologia e Botânica, Instituto de Biociências, Letras e Ciências Exatas (IBILCE), Universidade Estadual Paulista (UNESP), Rua Cristóvão Colombo 2265, CEP 15054-000, São José do Rio Preto-SP, Brazil.

Running title: Fine-scale microhabitat selection

*Corresponding author: G.Q. Romero; E-mail: gq_romero@yahoo.com.br

ABSTRACT

Although a wide variety of arthropods specialize on a specific host plant, little is known about the evolution of host–plant specialization in spiders. In several regions of South America, the Neotropical jumping spider *Psecas chapoda* associates with *Bromelia balansae*, a rosette-shaped plant that does not accumulate rain water in phytotelmata. We conducted experiments using bromeliad species with distinct architectures that were uncommon in the geographic range of *P. chapoda* to investigate the level of spider specialization in microhabitat structure. We also tested the influence of phytotelmata and foliar spines on host plant selection. *B. balansae*, *Ananas comosus* and *Aechmea distichantha* (tank-bromeliad), which share similar traits (e.g. long and narrow leaves), were colonized in similar frequencies. *Aechmea fasciata*, a tank-bromeliad that has short and broad leaves, was never colonized by these spiders, and *Aechmea blanchetiana*, tank-bromeliad with long and broad leaves, was only colonized infrequently. The removal of foliar spines did not affect the number of *P. chapoda* on *B. balansae*. Our findings suggest that microhabitat specialization by *P. chapoda* is based on rosette and leaf architectures. This unusual specialization likely evolved because the bromeliads with such architecture (i.e. B. balansae) typically dominate the biogeographic area of *P. chapoda*, and because this microhabitat provides specific benefits to spiders, as shelter, and as foraging and reproductive sites.

ADDITIONAL KEYWORDS: Bromeliaceae – host-plant selection – plant architecture – specific associations.

INTRODUCTION

Specializations in specific host plants have evolved among a wide variety of arthropods. For herbivorous insects, highly specific relationships with few host plant may be advantageous because of restrictions imposed by their natural enemies (Price *et al*., 1980; Coley & Barone, 1996), plant chemical defenses (Rhoades & Cates, 1976; Bernays & Graham, 1988; Schoonhoven, Jermy & Van Loon, 1998), low nutritional value (Bernays & Graham, 1988), or mechanical barriers (Howe & Westley, 1988). Less is known about the specific associations between plants and predatory arthropods. The mutualistic relationships between ants and myrmecophytic plants are to date the most studied examples of predator-plant associations. Factors favouring ant-plant specializations may include nesting space (e.g., domatia size) (Fonseca & Ganade, 1996) or specific host plant volatiles used as chemical cues for foundation queens. Although recent studies have reported associations of spiders with specific plant species and/or architecture (Romero, 2006; Vasconcellos-Neto *et al*., 2007), little is known about the ecological mechanisms that might favour microhabitat specialization in spider-plant systems (Romero, 2006).

Plants of the large Neotropical family Bromeliaceae have a complex architecture and many species have a cistern that collects rain water and thereby provides a suitable microhabitat for various arthropods and small vertebrates (Diesel, 1997; Eterovick, 1999; Cogni & Oliveira, 2003; Romero & Vasconcellos-Neto, 2005a, b; Romero, 2006). Associations between spiders and Bromeliaceae are especially common in Neotropical regions (Barth *et al*., 1988; Santos, Almeida & Nunes, 2002; Dias & Brescovit, 2004; Romero & Vasconcellos-Neto, 2004, 2005a, b, c; Romero, 2006; Romero *et al*., 2007). For example, all species of the genus *Cupiennius* (Ctenidae) are

closely associated with Bromeliaceae and Musaceae, on which they hide during the day, whereas, at night, they hunt, mate, and molt (Barth *et al.*, 1988). The spiders *Pachistopelma rufonigrum* (Theraphosidae) and *Nothroctenus fuxico* (Ctenidae) inhabit tank-bromeliads (i.e. bromeliads that accumulate rain water) in Northeastern Brazil and apparently use them as shelter against the high temperatures of the sandy soil, as well as a nursery for spiderlings (Santos *et al.*, 2002; Dias & Brescovit, 2004). Recent studies have reported tight associations between jumping spiders and bromeliads (Rossa-Feres *et al.*, 2000; Romero & Vasconcellos-Neto, 2004, 2005a, b, c; Romero, 2006) in several types of vegetation in Brazil, Bolivia, Argentina, and Paraguay (Romero, 2006). To date, *Psecas chapoda* (Salticidae) and the plant *Bromelia balansae* (Bromeliaceae) comprise the most thoroughly investigated example of spider–plant association (Romero, 2006). This system was recently reported to be mutualistic, where spiders use the plants as foraging and mating sites, substrate for egg sacs and nursery for spiderlings, as well as shelter against predators and fire (Romero & Vasconcellos-Neto, 2005a, b, c; Romero, 2006; G. Q. Romero, unpubl. data). The plant in turn benefits because the spiders provision *B. balansae* with the nitrogen derived from their debris (e.g. faeces, silk from egg sacs, prey carcass, exuviae), thus enhancing plant growth (Romero *et al.*, 2006).

Some jumping spiders (e.g. *Psecas* sp., *Eustiromastix nativo*, and *Coryphasia* spp.) are generalists and inhabit several bromeliad species. *Psecas chapoda* appears to specialize by inhabiting almost exclusively one host species (*B. balansae*) (Romero, 2006). Romero (2006) suggested that this phenomenon may reflect the availability of host plant species across the different habitats (phytophysiognomies) in different geographic regions. For example, although the generalist spiders occur in areas in

which the bromeliad flora was especially rich and diverse (e.g. coastal rain forests), the areas in which *P. chapoda* occurs (savannas and semi-deciduous forests) are dominated by *B. balansae* (Romero, 2006). Experimental introduction of other bromeliad species bearing different architecture (e.g. leaf and rosette shapes) can help clarify the underlying basis of the unusual specificity of *P. chapoda* for a particular bromeliad. If, in experiments, *P. chapoda* takes up residence in bromeliads of varied architecture, then this would suggest that specificity in the field is primarily a consequence of *B. balansae* being most available. However, if *P. chapoda* in experiments takes up residence primarily in bromeliads similar in architecture to *B. balansae*, then this would suggest that the specificity of *P. chapoda* to this bromeliad species is based on active choice by the salticid.

In the present study, we tested whether the specialization of *P. chapoda* in *B. balansae* occurs simply because other bromeliads are unavailable in its geographic region, or whether it can selects for specific plant architecture. The centre of *B. balansae*, which does not accumulate rain water, is frequently used as shelter by adult spiders and as a nursery for spiderlings (Romero & Vasconcellos-Neto, 2005a); thus, we investigated whether the presence of phytotelmata might negatively influence host plant choice by *P. chapoda*. In addition, Romero & Vasconcellos-Neto (2005a, c) suggested that the presence of large spines on *B. balansae* can protect adult and immature spiders against predators, such as birds and small mammals. Thus, we tested whether spines in leaf margins of the bromeliads influence host plant selection by *P. chapoda*.

MATERIAL AND METHODS

STUDY AREA AND ORGANISMS

This work was conducted in two semideciduous forest fragments (Vila Azul: 20°51′S; 49°22′W, Dahma: 20°48′S; 49°19′W) both in São José do Rio Preto city, São Paulo state. The climate type in the region is characterized by warm and wet summers and dry winters. Mean annual rainfall varies in the range 1100–1250 mm; the wet season (September to March) receives 85% of the annual rainfall, whereas the cold and dry season (April to August) receives only 15% (Barcha & Arid, 1971).

In the field, the jumping spider *P. chapoda* (Salticidae) associates exclusively with the plant *B. balansae* (Bromeliaceae) in a large geographic area that includes Paraguay, Bolivia, and four states in Brazil (Romero, 2006). We observed *P. chapoda* (in low frequency) in pineapple plantations (*Ananas comosus*) in three areas in São Paulo state (São José do Rio Preto, Dois Corregos, and Brotas cities); in the state of Rio Grande do Sul (Turvo Reserve, Derrubadas city), one individual of *P. chapoda* was found on the bromeliad *Aechmea distichantha* (Romero, 2006). The entire life cycle of *P. chapoda*, including courtship behavior, mating, egg sac deposition, and population recruitment of the young occurs almost exclusively on *B. balansae* (Rossa-Feres *et al*., 2000; Romero & Vasconcellos-Neto, 2005a, b). Populations of this species are mainly found on bromeliads in open areas, and rarely found on bromeliads from forest understories (Romero & Vasconcellos-Neto, 2005a, b). Dry leaves fallen from forest trees block the internal base of bromeliad rosettes, reducing the availability of shelter for adult spiders and entirely eliminating nurseries for spiderlings (Romero & Vasconcellos-Neto, 2005a). In addition, *P. chapoda* occurs in low frequency on bromeliads bearing inflorescences. During the reproductive season, the architecture of

B. balansae changes from a conical tridimensional configuration to an almost bidimensional one, due to leaf-fall that exposes the flowers to pollinators (e.g. hummingbird). With this architecture, the spiders would be more exposed to external factors such as predation and climatic adversity (Romero & Vasconcellos-Neto, 2005a).

EXPERIMENT I: COLONIZATION OF PLANTS WITH DISTINCT ARCHITECTURE

To investigate the colonization of *P. chapoda* on plants with distinct architecture, we conducted a randomized block experiment on the margins of a semideciduous forest fragment (Vila Azul). Each block consisted of three plants, and each plant was a different bromeliad species: *B. balansae*; *Ananas comosus* (pineapple), a species which shares similar morphological traits with *B. balansae*; and *Aechmea fasciata*, which differs from *B. balansae* in plant architecture (Table 1, Fig. 1). *Bromelia balansae* and *A. comosus* do not accumulate rain water (i.e. phytotelmata absent), both have long and narrow leaves, and their leaf margins are covered with spines. However, the spines of *A. comosus* are smaller and more numerous. By contrast, *A. fasciata* has short, wide leaves forming a phytotelmata that accumulates rain water, and short marginal spines on leaf margins.

Each experimental block (N = 20) was 4–20 m from its nearest neighbor, and 0.3–0.5 m separated the plants into each block. The *Bromelia balansae* plants that we used in the experiment were collected in other areas, the rationale for this being to minimize the impact of collecting on plant and spider populations. Individuals of *A. comosus* were collected from plantations in Fronteira, Minas Gerais state. Individuals of *A. fasciata* were obtained from a specialized flower shop (CEASA/Campinas city). For

each plant in the experiment, we randomly selected one leaf from the median layer for measuring its length and base width; we also counted the total number of leaves on each plant. The study began on 13 January and ended on 23 February 2006.

Before the experiment began, all plants were inspected and all spiders, egg sacs, and webs were removed. Afterwards, plants were inspected every 10–15 days and all spiders and egg sacs found were censused on each plant. Age-specific patterns of spot and coloration were used to identify *P. chapoda* instars as spiderlings (third instar), young (fourth and fifth), juvenile males and females (sixth instar), subadult males (seventh instar), or adult males (eight instar) (Romero & Vasconcellos-Neto, 2005b). We included subadult and adult females (seventh and eight instars) in the same class for analysis, because both instars have the same coloration pattern and body size up to 1.6 cm in length (Romero & Vasconcellos-Neto, 2003).

EXPERIMENT II: COLONIZATION OF PLANTS WITH AND WITHOUT PHYTOTELMATA

By conducting a randomized block experiment at Dahma farm using *B. balansae* and *A. distichantha* plants, we investigated whether *P. chapoda* specialization is restricted to bromeliads that do not bear phytotelmata (Table 1). Each experimental block consisted of one *B. balansae* and one *A. distichantha* (N = 19); they were 4–20 m from their nearest neighbors and 0.3–0.5 m from other plants in each block. *Aechmea distichantha* was used because its morphological features are similar to those of *B. balansae* (Fig. 1); however, these differ in that the leaf base of *A. distichantha* has a lateral expansion that forms a phytotelmata.

Before the experiment began, all *B. balansae* plants were inspected to ensure that they had not already been colonized by *P. chapoda* (individuals and eggsacs). Plants were inspected every 3–7 days from 13 December 2006 to 6 January 2007 and all spider species were censused. This experiment was repeated at Vila Azul from 6 January to 7 February 2007, using the same procedure and plant species described above. However, a new bromeliad species, *Aechmea blanchetiana*, was added to the block. This species bears phytotelmata and shares architecture (e.g. leaf length and width) intermediate to *B. balansae* and *A. fasciata* (Fig. 1, Table 1). *Aechmea distichantha* and *A. blanchetiana* were obtained at specialized flower shops (CEASA/Campinas city); *B. balansae* were collected from the study area.

EXPERIMENT III: THE ROLE OF LEAF SPINES IN *B. BALANSAE*

In this experiment, we removed the spines from *B. balansae* leaves to test whether *P. chapoda* prefers plants with spines over plants with their spines removed. Thirty *B. balansae* plants growing naturally in the field (Dahma farm) were randomly selected and numbered. These plants were similar in size, were in open areas and each was at least 30 cm from its nearest neighbor. Each plant was randomly selected to receive a treatment: plants with all spines removed and plants with intact spines (control) (Table 1). Leaves of the control plants were gently shaken to simulate the vibrations caused by removing the spines from the experimental plants. All spiders and egg sacs present at the beginning of the experiment were censused (pre-treatment data). Plants were monitored every 3–7 days, and all spiders and egg sacs found were censused. The removal of spines did not cause conspicuous damage on leaves. The experiment was conducted from 22 September to 31 October 2006. Three experimental

plants flowered on 16 November, and so these plants were excluded from following samples because *P. chapoda* do not colonize reproductive bromeliads (Romero & Vasconcellos-Neto, 2005a); on 30 November, two other plants were excluded from the experiment for the same reason.

STATISTICAL ANALYSIS

A randomized-block experimental design was used for experiments I and II; in experiment III we used a completely randomized design (Hurlbert, 1984). The total number of spiders on bromeliads from experiments I and II was compared between treatments using randomized block, repeated measures analysis of variance (ANOVA) (Sokal & Rohlf, 1995), in which blocks were the random effects, treatments were the fixed effects, and time was the repeated factor. Data on experiment III were compared using repeated measures ANOVA. Although data from the three experiments did not show normal distribution, even after logarithmical transformation, their variances were homogeneous. Therefore, the data were $\log_{10}(N + 1)$ transformed and then parametric tests were used. The probabilities of the within-subject factors for all repeated measures analyses were tested for sphericity using the Mauchley's test of sphericity; if necessary, the Greenhouse–Geisser epsilon correction was used (Sokal & Rohlf, 1995). Occurrence frequencies of *P. chapoda* instars in different plant species were compared using G-test in a contingency table (Sokal & Rohlf, 1995). All analyses of variance were run using Type III sums of squares (SS) in general linear models (GLM) and all experiments had a balanced design. Data are presented as the mean ± SE, as computed directly from untransformed data.

Some parameters, such as leaf length (LL), leaf width (LW), LL : LW ratio, and leaf number (LN) of the bromeliad species used in the experiments (i.e. *B. balansae*, *A. comosus*, *A. fasciata*, *A. distichantha*, and *A. blanchetiana*) were compared using ANOVA/Fisher's least significant difference post-hoc tests or t-tests (Table 1). Additionally, we performed discriminant analysis to characterize rosette architecture and to show what plant traits best discriminate the bromeliad species. The analysis was carried out using LL, LW, LL : LW ratio, and LN. The results of this analysis are presented in Fig. 1. The first canonical variable (factor 1) better discriminated the species (eigenvalue of factor 1 = 19.6; eigenvalue of factor 2 = 2.07). The analysis classified correctly all species (100% of *A. blanchetiana* and *A. comosus*, 90% of *A. distichantha*, 92% of *B. balansae*, and 80% of *A. fasciata*). The most important parameter that discriminated the groups was leaf width (F-statistic: LW = 173.8, LL = 54.4, LN = 11.47, LL:LW = 36.1).

RESULTS

The total number of *P. chapoda* individuals did not differ statistically between plants of *B. balansae* and *A. comosus* (ANOVA: P = 0.068; Fig. 2A, Table 2). However, although immature *P. chapoda* (third to sixth instars) occurred at similar frequencies on different bromeliad species (G-test: P ≥ 0.1; Table 3), the frequency of adults and subadults (seventh and eighth instars) was higher on *A. comosus* than on *B. balansae* (G = 13.46, d.f. = 1, P < 0.001; Table 3). *Bromelia balansae* had narrower leaves than *A. comosus* (Table 1), probably because of stress-induced withering of the leaves of some *B. balansae* individuals during the experiment. We never found *P. chapoda* on *A. fasciata* (Fig. 2A), and it is of interest that *A. fasciata* has broad and short leaves (Table

1, Fig. 1). Although *B. balansae* and *A. comosus* had narrow and elongated leaves, *A. fasciata* had broad and short leaves (Table 1, Fig. 1). Yet other spiders (especially spiders from the families Theridiidae, Anyphaenidae, Salticidae, and Gnaphosidae) were found in all three of this bromeliads species (Fig. 2B) and their numbers increased significantly over time on *A. fasciata* (P = 0.002; Table 2).

Numbers of *P. chapoda* on plants with (*B. balansae*) or without phytotelmata (*A. distichantha*) did not differ statistically at Dahma farm (P = 0.419; Fig. 3A, Table 2). This was observed for adults and subadults (G = 2.0, d.f. = 1, P = 0.157; Table 3); however, immatures (fifth and sixth instars) occurred more frequently on *B. balansae* (G-test; P < 0.001; Table 3). Our results from Vila Azul were similar: the pattern of plant colonization by *P. chapoda* was similar for *B. balansae* and *A. distichantha* (Fig. 3B). However, the number of *P. chapoda* individuals was lower on *A. blanchetiana* than on the former two plant species (Fig. 3B) (P = 0.003; Table 2). Similarly, adults, subadults and the immature (sixth instar) were significantly more common on *B. balansae* and *A. distichantha* than on *A. blanchetiana* (G-test; P ≤ 0.003). Discriminant analysis showed that *A. blanchetiana* is distinct from *B. balansae* and *A. distichantha*; it bears intermediate architecture between *A. fasciata* (from the first experiment) and the reminder species (Fig. 1). Although *B. balansae* had the longest and narrowest leaves, *A. blanchetiana* had the widest leaves and *A. distichantha* had the highest number of leaves at Dahma (Table 1).

The number of spiders on plants with intact or removed spines did not differ statistically (P = 0.243; Fig. 4, Table 2), nor did the architectural parameters of plants differ statistically (Table 1).

When observers approached of bromeliads that lack phytotelmata (e.g. *B. balansae* and *A. comosus*), *P. chapoda* ran quickly to the base of the rosette. However, when occupying tank-bromeliads (*A. distichantha* and *A. blanchetiana*), the spiders' strategy to escape was different: they ran amidst leaves and from adaxial to abaxial leaf surfaces, but never entered the phytotelmata.

DISCUSSION

Over a large part of South America, *P. chapoda* inhabits *B. balansae* plants almost exclusively (Romero, 2006). For a spider, this is unusual fidelity for a specific substratum. In the present study, we have shown that this microhabitat fidelity persisted even after the introduction of other bromeliad species bearing different morphological traits, such as *A. fasciata*. By determining the frequency with which *P. chapoda* colonized certain bromeliads (e.g. *B. balansae*, *A. comosus*, and *A. distichantha*) that shared morphological traits (i.e. long and narrow leaves; Fig. 1), we suggest that this spider specialization is related to microhabitat structure rather than to plant taxonomy. The low frequency of *P. chapoda*, especially adults, subadults and sixth instars, on one of the bromeliads (i.e. *A. blanchetiana*) that has architecture intermediate between *A. fasciata* and the three occupied species (i.e. *B. balansae*, *A. distichantha*, and *A. comosus*) supports our microhabitat-specificity hypothesis. The factors that drove this spider species to extreme specialization are still poorly understood, and might be related to the large local availability of a substratum bearing specific architecture (i.e. *B. balansae*) that provides numerous benefits to the spiders (see Romero & Vasconcellos-Neto, 2005a; Romero, 2006).

Adults and subadults, but not younger spiders, occur in higher frequency on bromeliads with wider leaves (i.e. *A. comosus*) than on those with narrower leaves (i.e. *B. balansae*). Narrow leaves may limit space for larger, but not smaller spiders. Space limitation has been reported as important in other predator–plant interactions, such as Amazonian ant-myrmecophyte systems (Fonseca & Ganade, 1996). Therefore, the width of *A. fasciata* leaves, which are much larger than that of *A. comosus* could provide better foraging sites for spiders, thus explaining the higher abundance of diverse spider species on these leaves in our experiment. However, *P. chapoda* never colonized this plant species. Some morphological features of the rosette may be disadvantageous for this spider species. For example, leaf concavity in *A. fasciata* is less pronounced than that in *B. balansae*, *A. comosus*, or *A. distichantha*. *Psecas chapoda* frequently uses concavities for shelter, and adult females constructed their egg sacs on the concave side of leaves and covered them with a plain silken cover attached to the edges of the leaf (Rossa-Feres *et al*., 2000). Additionally, *A. fasciata* leaves are usually bentdown and thus differ from the erect leaves of the plants used by *P. chapoda*. Such morphological traits may somehow hinder courtship. Males stand on the upper parts of leaves, with females tending to remain in the base of the rosette (Rossa-Feres *et al*., 2000). During courtship, males occupy the upper part of the leaf, whereas the females remain in the base of the rosette (Rossa-Feres *et al*., 2000). The bending leaves of *A. fasciata* might hinder visual contact between the male and female. The base of *B. balansae* rosettes do not accumulate rain water and this maybe why they frequently serve as nurseries for newly-emerged *P. chapoda* spiderlings, and as shelter and rest sites (Romero & Vasconcellos-Neto, 2005a, b, c). In spite of this, there was no evident difference in the density of *P. chapoda* did not differ between plants with or without

phytotelmata. This result suggests that *P. chapoda* do not recognize the presence of phytotelmata or that this plant parameter is not taken into account by the spider when evaluating host plants. Contrasting results were found by Romero & Vasconcellos-Neto (2005a), who showed that *P. chapoda* preferentially occupy *B. balansae* that do not accumulate the dry leaves fallen from trees. This may be because debris blocks the bromeliad base and reduces the availability of shelters and nurseries. Water in the phytotelm bromeliads could function analogously to dry leaves in hindering the spider's access spider access to shelters. Our results suggest that *P. chapoda* does not recognize the water in phytotelm bromeliads as a barrier because the spider population studied here did not evolve in areas with tank-bromeliads. However, in an area (Derrubadas city) where *A. distichantha* and *B. balansae* occur in sympatry, *P. chapoda* were rarely found on the former plant, although frequently found on the latter (Romero, 2006: table 1), suggesting that populations that evolved in sites with tank-bromeliads may recognize and avoid the microhabitat created by this plant.

When on bromeliads that lack phytotelmata, *P. chapoda* individuals that have been disturbed runn quickly to the base of the rosette. However, when occupying tank-bromeliads, they never enter the phytotelmata. By contrast, other bromeliad-living salticids (e.g. *Psecas* sp., *Coryphasia monteverde*, *C. cardoso*, *Eustiromastix nativo*) that inhabit certain tank-bromeliads, including *A. distichantha* and *A. blanchetiana* in other geographic regions (Romero, 2006), enter the water of the phytotelmata and can remain submerged for a few minutes (Romero *et al*., 2007; G. Q. Romero, unpubl. data), suggesting that bromeliad-dwelling jumping spiders inhabiting tank-bromeliads are adapted to submersion, and that *Psecas chapoda*, having evolved in geographic regions where tank-bromeliads are absent or rare, lacks a similar adaptation.

The large spines at the margins of *B. balansae* leaves may protect spiders against vertebrate predators (e.g. birds and small mammals) (Romero & Vasconcellos-Neto, 2005b). If this hypothesis is true, then spiders might select plants with spines in preference to plants lacking spines. However, presence of spines was not a plant parameter used by spiders in host plant evaluation and selection.

This is one of only a few studies to demonstrate host plant selection by a spider. Microhabitat specialization by *P. chapoda* seems to be restricted to certain architectural features of their host plant rosettes; these spiders apparently use leaf length and width as cues to evaluate their hosts, or both. However, neither phytotelmata, nor spines appeared to influence plant choice by this spider species. Our results clearly show that *P. chapoda* evaluates the fine-scale physical structure of its microhabitat.

REFERENCES

Barcha SF, Arid FM. 1971. Estudo da evapotranspiração na região norte-ocidental do estado de São Paulo. *Revista de Ciências* **1:**99-122.

Barth FG, Seyfarth EA, Bleckmann H, Schüch W. 1988. Spiders of the genus *Cupiennius* Simon 1891 (Araneae, Ctenidae). I. Range distribution, dwelling plants, and climatic characteristics of the habitats. *Oecologia* **77:**187-193.

Bernays EA, Graham M. 1988. On the evolution of host specificity in phytophagous arthropods. *Ecology* **69:**886-892.

Cogni R, Oliveira PS. 2003. Patterns in foraging and nesting ecology in the neotropical ant, *Gnamptogenys moelleri* (Formicidae, Ponerinae). *Insectes Sociaux* **51:**123-130.

Coley PD, Barone JA. 1996. Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics* **27:**305-335.

Dias SC, Brescovit AD. 2004. Microhabitat selection and co-occurrence of *Pachistopelma rufonigrum* Pocock (Araneae; Theraphosidae) and *Nothroctenus fuxico* new species (Araneae, Ctenidae) in tank bromeliads from Serra de Itabaiana, Sergipe, Brazil. *Revista Brasileira de Zoologia* **21:**789-796.

Diesel R. 1997. Maternal control of calcium concentration in the larval nursery of the bromeliad crab, *Metopaulias depressus* (Grapsidae). *Proceedings of the royal society of London series B-Biological Sciences* **264:**1403-1406.

Eterovick, PC. 1999. Use and sharing of calling and retreat sites by *Phyllodytes luteolus* in a modified environment. *Journal of Herpetology* **33:**17-22.

Fonseca CR, Ganade G. 1996. Asymmetries, compartment and null interactions in an Amazonian ant-plant community. *Journal of Animal Ecology* **65:**339-347.

Howe HF, Westley LC. 1988. *Ecological relationships of plants and animals*. New York: Oxford University Press. 273p

Hurlbert SH. 1984. Pseudoreplication and design of ecological field experiments. *Ecological Monographs* **54:**187-211.

Price PW, Bouton CE, Gross P, Mcpheron BA, Thompson JN, Weis AE. 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annual Review of Ecology and Systematics* **11:**41-65.

Rhoades DF, Cates RG. 1976. Toward a general theory of plant antiherbivore chemistry. *Recent Advances in Phytochemistry* **10:**168-213.

Romero GQ. 2006. Geographic range, habitats and host plants of bromeliad-living jumping spiders (Salticidae). *Biotropica* **38:**522–530.

Romero GQ, Vasconcellos-Neto J. 2003. Natural history of *Misumenops argenteus* Rinaldi (1988) (Araneae, Thomisidae): seasonality and diet on *Trichogoniopsis adenantha* (Asteraceae). *Journal of Arachnology* **31:**297-304.

Romero GQ, Vasconcellos-Neto J. 2004. Spatial distribution patterns of jumping spiders associated with terrestrial bromeliads. *Biotropica* **36:**596-601.

Romero GQ, Vasconcellos-Neto J. 2005a. The effects of plant structure on the spatial and microspatial distribution of a bromeliad-living jumping spider (Salticidae). *Journal of Animal Ecology* **74:**12-21.

Romero GQ, Vasconcellos-Neto J. 2005b. Spatial distribution and microhabitat preference of *Psecas chapoda* (Peckham & Peckham) (Araneae, Salticidae). *Journal of Arachnology* **33:**124-134.

Romero GQ, Vasconcellos-Neto J. 2005c. Population dynamics, age, structure and sex ratio of the bromeliad-dwelling jumping spider, *Psecas chapoda* (Salticidae). *Journal of Natural History* **39:**153-163.

Romero GQ, Mazzafera P, Vasconcellos-Neto J, Trivelin PCO. 2006. Bromeliad-living spiders improve host plant nutrition and growth. *Ecology* **87:**803-808.

Romero GQ, Santos AJ, Wienskoski EH, Vasconcellos-Neto J. 2007. Association of two new *Coryphasia* species (Araneae, Salticidae) with tank-bromeliads in southeastern Brazil: habitats and patterns of host plant use. *Journal of Arachnology* (in press).

Rossa-Feres D de C, Romero GQ, Gonçalves-de-Freitas E, Feres RJF. 2000. Reproductive behavior and seasonal occurrence of *Psecas viridipurpureus* (Salticidae, Ananeae). *Brazilian Journal of Biology* **60:**221-228.

Santos RL, Almeida MG, Nunes JV. 2002. Notes on the association of *Pachistopelma rufonigrum* Pocock 1901 (Theraphosidae) with phytotelm bromeliads in eastern Rio Grande do Norte State, NE-Brazil. *Journal of the Bromeliad Society* **52:**22-124.

Schoonhoven LM, Jermy T, Van Loon JJA. 1998. *Insect-plant biology*. Chapman & Hall, London.

Sokal RR, Rohlf FJ. 1995. *Biometry: the principles and practice of statistics in biological research*. Third edition. W. H. Freeman and Company, New York, USA.

Vasconcellos-Neto J, Romero GQ, Santos AJ, Dippenaar-Schoeman AS. 2007. Associations of spiders of the genus *Peucetia* (Oxyopidae) with plants bearing glandular hairs. *Biotropica* **39:**221-226.

Table 1. Mean (± 1 SE) of leaf length (LL), leaf width (LW), LL:LW ratio and leaf number (LN), as well the presence or absence of phytotelmata (Phy) of the bromeliads used in the experiments I, II and III. Different letters indicate statistical differences [experiments I and II (Vila Azul): one way ANOVA/Fisher LSD; experiments II (Dahma) and III: t-test, α=0.05].

Bromeliads	LL	LW	LN	LL:LW	Phy	N
Experiment I - distinct architectures						
B. balansae	71.25±2.65 a	2.63±0.06 a	17.10±0.85 a	27.28±4.93 a	Absent	20
A. comosus	59.50±2.11 b	4.56±0.13 b	19.65±0.93 b	13.27±2.77 b	Absent	20
A. fasciata	28.00±1.40 c	8.35±0.24 c	15.20±0.84 a	3.41±0.91 c	Present	20
Experiment II - presence/absence of phytotelmata (Dahma)						
B. balansae	77.21±2.82 a	2.25±0,09 a	20.94±1.27 a	35.10±70 a	Absent	19
A.distichantha	58.47±2.74 b	1.17±0.09 b	28.89±1.07 b	35.73±12.1 a	Present	19
Experiment II - presence/absence of phytotelmata (Vila Azul)						
B. balansae	102.14±10.12 a	2.27±0.09 a	25.81±1.70 ab	44.57±13.45a	Absent	11
A.distichantha	58.36±2.49 b	1.62±0.07 b	29.54±2.65 a	36.65±7.73 a	Present	11
A.blanchetiana	36.86±3.11 c	6.38±0.17 c	19.45±2.67 b	5.86±1.81 b	Present	11
Experiment III - leaf spines						
Intact spines	106.10±4.60 a	1.97±0.15 a	27.93±1.90 a	56.7±13.61 a	Absent	15
Removed spines	104.70±6.54 a	1.98±0.13 a	27.00±2.10 a	54.9±13.14 a	Absent	15

36

Table 2. Randomized block, repeated measures ANOVAs examining the number of spiders on bromeliads in the experiments I, II and III, which tested, respectively, the influence of varying architecture, presence of phytotelmata, and presence of spines on the leaf margins on the spider colonization. See Table 1 for the bromeliad species used in each experiment.

Experiments	Source of variation	d.f.	MS	F	P
Experiment I - distinct architectures (*Psecas chapoda*)					
	Treatment	1	0.061	2.015	0.068
	Error	19	0.030		
	Time	3	0.023	0.897	0.448
	Time x treatment	3	0.013	0.489	0.691
	Error	57	0.0258		
Experiment I - distinct architectures (other species)					
	Treatment	2	0.194	7.279	0.002
	Error	38	0.028		
	Time	3	0.163	7.455	<0.001
	Time x treatment	6	0.046	2.093	0.059
	Error	114	0.022		
Experiment II - presence/absence of phytotelmata (Dahma)					
	Treatment	1	0.022	0.684	0.419
	Error	18	0.032		
	Time*	6	0.190	8.631	<0.001
	Time x treatment**	6	0.028	1.253	0.285
	Error	108	0.022		
Experiment II - presence/absence of phytotelmata (Vila Azul)					
	Treatment	2	0.304	7.813	0.003
	Error	20	0.039		
	Time	6	0.027	1.392	0.223
	Time x treatment	12	0.014	0.701	0.748
	Error	120	0.020		
Experiment III - leaf spines					
	Treatment	1	0.065	1.191	0.243
	Error	23	0.054		
	Time	7	0.024	1.330	0.243
	Time x treatment	7	0.034	1.862	0.079
	Error	161	0.018		

G-G correction for sphericity: * P < 0.001; ** P = 0.296

Table 3. Number of individuals of *P. chapoda* of different instars on the bromeliads of experiments I and II. Values inside parentheses indicate the percentage of individuals of each instar.

Experiments	Instars of *Psecas chapoda*				
	3rd	4th	5th	6th	7+8th
Experiment I - distinct architectures					
Bromelia balansae	0	11(55)	28(62.22)	14(40)	1(6.67)
Ananas comosus	0	9(45)	17(37.78)	21(60)	14(93.33)
Aechmea fasciata	0	0	0	0	0
Experiment II - presence/absence of phytotelmata (Dahma)					
Bromelia balansae	1(75)	3(42.86)	17(62.96)	29(61.70)	25(41)
Aechmea distichantha	3(25)	4(57.14)	10(37.04)	18(38.30)	36(59)
Experiment II - presence/absence of phytotelmata (Vila Azul)					
Bromelia balansae	3(33.33)	3(37.5)	5(35.71)	22(53.66)	15(38.46)
Aechmea distichantha	6(66.66)	2(25)	4(28.58)	16(39.02)	22(56.41)
Aechmea blanchetiana	0	3(37.5)	5(35.71)	3(7.32)	2(5.13)

Figure captions

Fig. 1. Relationship between scores of factors 1 and 2 for the discriminant analysis of plant traits.

Fig. 2. Number of individuals of (A) *Psecas chapoda* and of (B) other spider species on bromeliads of varying architecture. Beginning of the experiment: January 13 2006; samples: 1 = January 20, 2 = February 2, 3 = February 14, 4 = February 23 2006. Error bars are ± 1 standard error.

Fig. 3. Number of individuals of *Psecas chapoda* on bromeliads with phytotelmata (*A. distichantha, A. blanchetiana*) and without phytotelmata (*B. balansae*) in two different areas (A = Dahma; B = Vila azul). The beginning of the experiment at Dahma and Vila Azul were December 11 2006 and January 4 2007 respectively. Samples for Dahma: 1 = December 13, 2 = December 16, 3 = December 19, 4 = December 23, 5 = December 27 2006, 6 = January 30 2007. Samples for Vila Azul: January 6, 2 = January 10, 3 = January 12, 4 = January 16, 5 = January 24, 6 = January 31, 7 = February 7 2007. Error bars are ± 1 standard error.

Fig. 4. Number of individuals of *Psecas chapoda* on plants of *Bromelia balansae* with spines intact and removed. Beginning of the experiment (pre-treatment): September 22 2006; samples: 1 = September 26, 2 = September 29, 3 = October 2, 4 = October 5, 5 = October 9, 6 = October 16, 7 = October 24, 8 = October 31. Error bars are ± 1 standard error.
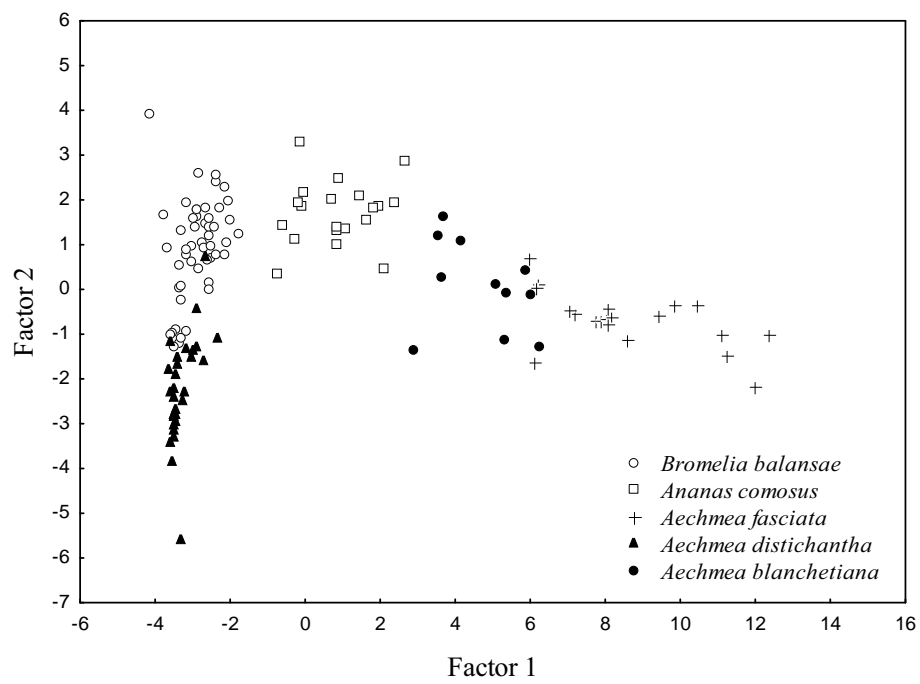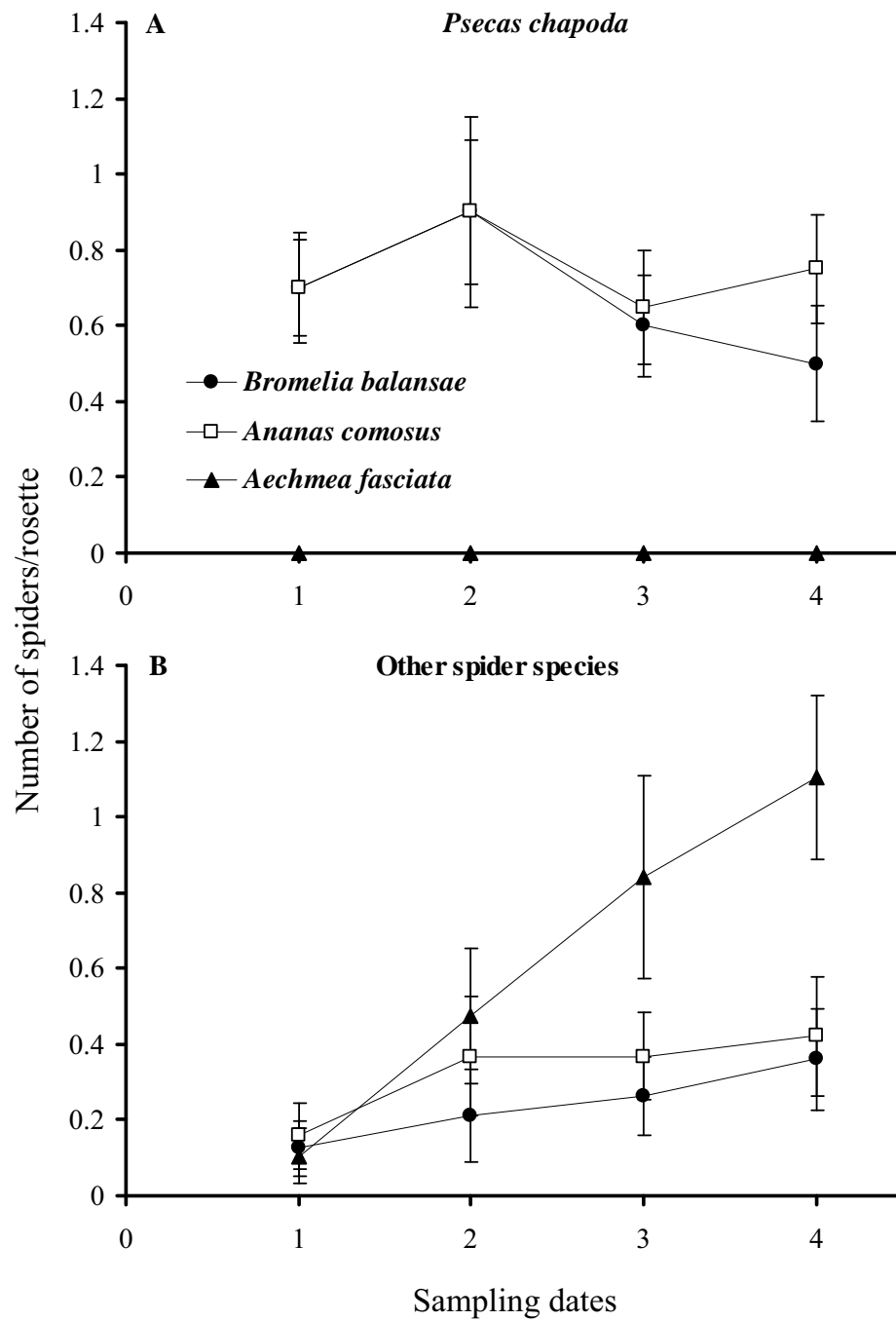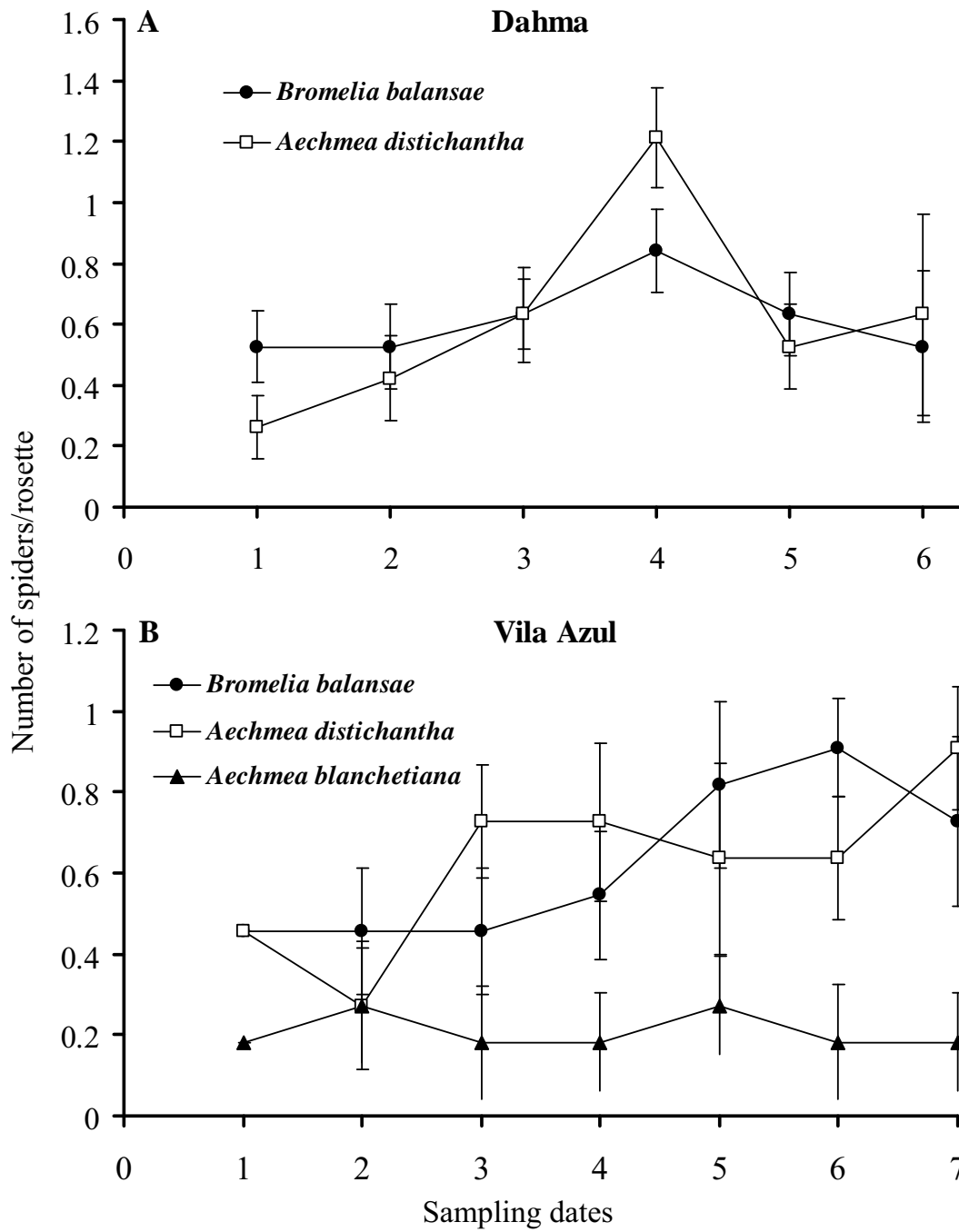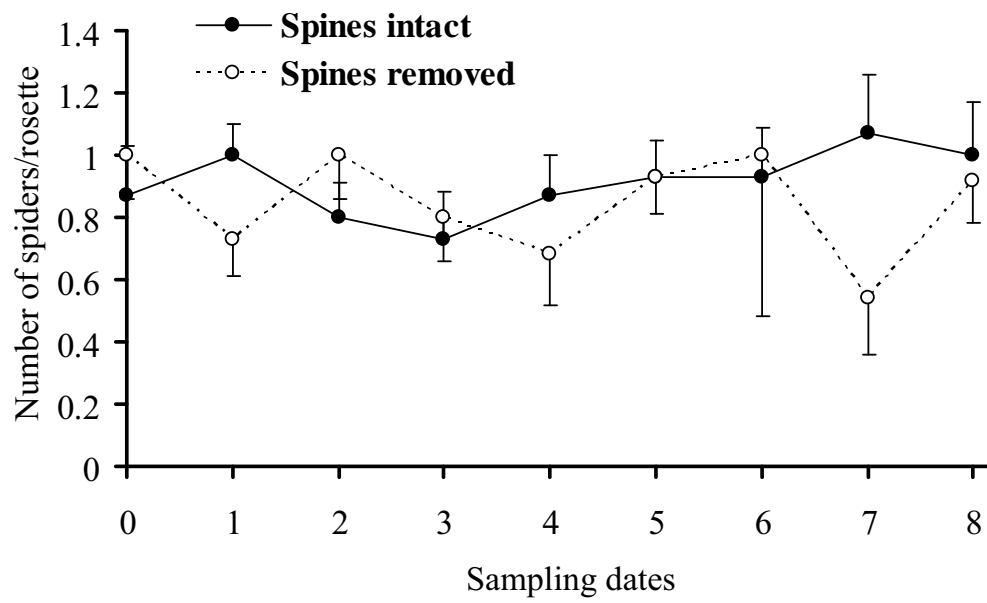
Fig. 1

Fig. 2

Fig. 3

Fig. 4

Omena, P.M. & Romero, G.Q.
Using visual cues of microhabitat traits to find home:
the case study of a bromeliad-living jumping spider (Salticidae)
(Manuscrito não publicado)

Using visual cues of microhabitat traits to find home: the case study of a bromeliad-living jumping spider (Salticidae)

Paula M. de Omena[1] and Gustavo Q. Romero[2]*

1. Pós-graduação em Biologia Animal, Instituto de Biociências, Letras e Ciências Exatas (IBILCE), Universidade Estadual Paulista (UNESP), Rua Cristóvão Colombo 2265, CEP 15054-000, São José do Rio Preto-SP, Brazil.

2. Departamento de Zoologia e Botânica, Instituto de Biociências, Letras e Ciências Exatas (IBILCE), Universidade Estadual Paulista (UNESP), Rua Cristóvão Colombo 2265, CEP 15054-000, São José do Rio Preto-SP, Brazil.

Running title: Visual cues and host plant selection

*Corresponding author: G.Q. Romero; E-mail: gq_romero@yahoo.com.br

ABSTRACT

Using visual cues of microhabitat traits to find home: the case study of a bromeliad-living jumping spider (Salticidae)

Spiders are selective for microhabitat and foraging sites, especially regarding the physical structure of host plants. Yet, little is known about which sensorial mechanisms they use to evaluate and select substrata. In this study, we manipulated real plants and plants' photos to test which plant traits are used by the bromeliad-dwelling spider *Psecas chapoda* to find their hosts, and whether this selection is based on visual (i.e., shape, color) or tactile stimuli. We further examined if *Psecas* is able to recognize its preferred substratum when placed on plants with different architectures. Our results showed that *Psecas* uses visual cues to find its preferred microhabitat. Rosette shaped monocots (Agavaceae) was preferred over other monocots and dicots. In both experiments involving real bromeliads and black-and-white bromeliad pictures choice was restricted to rosettes having narrow and long leaves. However, spiders delayed to select bromeliad pictures, suggesting that selection is primarily based on plant morphological traits, but color may also play a significant role in plant choice. Females remained longer than males on experimental bromeliads. Males detected bromeliad architecture on photos faster than females. Since males are likely to be more vulnerable to predation than females, they may have developed a more accurate vision allowing them to find shelter more efficiently. The great visual acuity of *P. chapoda* associated with the widespread availability of *B. balansae* might have lead to the evolution of this unusual spider-plant association. *Key words*: Bromeliaceae, visual selection, visual cues, host plant selection, plant architecture, Salticidae.

INTRODUCTION

Animals are usually distributed in a non-random manner in space and are expected to select microhabitats in order to increase their survival and reproductive success (Orians and Wittenberger 1991; Pulliam and Danielson 1991). Although spiders that live on plants are known for being selective in microhabitat and foraging sites, especially in relation to the physical structure of plants (Gunnarsson 1996; Halaj, Ross, and Moldenke 2000; Romero and Vasconcellos-Neto 2005a; Morse 2007), little is known about which sensorial mechanisms (i.e., visual, olfactory and tactile) they use to evaluate and select substrata. Some studies have shown that spiders can select a substratum based on color (Greco and Kevan 1994; Heiling et al. 2005), on odor (Aldrich and Barros 1995; Krell and Krämer 1998; Heiling, Cheng, and Herberstein 2004), on texture (Morse 1988; Greco and Kevan 1994) or on the frequency of prey visits (Morse 2007 and references therein). To date, most of the studies related to substratum choice by spiders refers to the optimal foraging theory, in which the choice is based on the amount of food resources to which spiders can obtain (e.g., Morse 2007 and references therein). However, little is known about choices displayed by spiders that spend entire life cycle on specific host plants (Romero 2006; Vasconcellos-Neto et al. 2007).

Recent studies have reported that several spider taxa live exclusively associated to specific plant types and use them not only as foraging sites (e.g., Romero, Souza, and Vasconcellos-Neto 2008), but also as sites for breeding, nursery for spiderlings, and as shelter against natural enemies and harsh climatic conditions (Dias and Brescovit 2003; Romero and Vasconcellos-Neto 2004 b, 2005, a, b, c; Romero 2006; Vasconcellos-Neto et al. 2007). For instance, in some regions of South America, nine species of jumping

spiders (Salticidae) were reported to live strictly associated to bromeliads (Romero and Vasconcellos-Neto 2004b, 2005a, b, c; Romero 2006). Whereas some jumping spiders (e.g. *Psecas* sp., *Eustiromastix nativo*, and *Coryphasia* spp.) are generalist, dwelling on several bromeliad species, the species *Psecas chapoda* uses almost exclusively only one host species, *Bromelia balansae* (Romero 2006). The evolution of *P. chapoda* specialization for this single host species possibly occurred because this spider inhabits areas (savannas and semi-deciduous forests) dominated only by *B. balansae*, which has long and narrow leaves (Romero 2006; Omena and Romero 2008). When bromeliad species bearing a similar (i.e., narrow and long leaves) or a different architecture (i.e., wide and short leaves) from the host *B. balansae* was experimentally introduced, *P. chapoda* colonized all the formers, but not the later ones. Thereby, it is likely that *P. chapoda* use certain architectural features to select their host plant rosettes, rather than selecting a specific plant species (Omena and Romero 2008). Although the existence of specific associations between spiders and plants depends on the ability of spiders to find their hosts, to our knowledge there is no experimental study reporting active host plant choice in jumping spiders as well as the stimuli and cues used by these animals to find their hosts.

Jumping spiders are among the most vision-dependent animals (Land 1969a). The visual sense controls much of their activities, such as orientation to prey capture (Hill 1979; Tarsitano and Andrew 1999; Tarsitano, Jackson, and Kirchner 2000; Li and Lim 2005; Tarsitano 2006), courtship (Jackson 1977; Lim, Land, and Li 2007), escape and agonistic behavior (Taylor et al. 2000; Li, Yik, and Seah 2002). It has been suggested that such an acute vision could have been essential for the evolution of these complex behaviors in Salticidae (Jackson 1992; Jackson and Pollard 1996; Lim and Li

2006; Lim, Land, and Li 2007). Visual sense can also control substrata choice by salticids and even contribute to specialization and evolution for specific microhabitats, such as bromeliads. However, to date there is no study showing that jumping spiders use their complex visual system to find their preferred habitats.

In this study we manipulated real plants and plants' photos to investigate if the bromeliad-dwelling jumping spider *P. chapoda* uses visual cues of plants traits to select microhabitat. We further examined whether *P. chapoda* recognizes a preferred host when experimentally placed on diverse plants with different architectures. This spider-plant association was recently reported to be mutualistic (Romero et al. 2006), so information on host plant choice can help understanding the evolution of this spider-plant mutualism. Specifically, we addressed the following questions: (1) Does *P. chapoda* recognize and visually select plants bearing rosette architecture? (2) Does this spider distinguish visually their host plant (i.e., *B. balansae*) or plants bearing similar architecture from other bromeliad species? (3) Do males and females of *P. chapoda* present the same pattern of host plant selection? (4) Do males and females spent different amount of time to select host plants? (5) Once on a plant, is *P. chapoda* able to indentify whether it is its preferred host?

METHODS

Organisms

The jumping spider *Psecas chapoda* is commonly found associated with *B. balansae* in several regions of South America (Romero 2006). The entire life cycle of *P. chapoda*, including courtship behavior, mating, egg sac deposition and population recruitment of the young occurs almost exclusively on this bromeliad (Rossa-Feres et al. 2000;

Romero and Vasconcellos-Neto 2005a, b). The central concavity of the leaves is used as shelter by the spiders and as site where females deposit egg sacs. The egg sacs are wrapped in a plain silk cover (nest) that is spun at the edge of each leave (Rossa-Feres et al. 2000; Vieira and Romero 2008). The structure of the leaves is also utilized during courtship; females remain in the base of the rosette, whereas males occupy the upper part of the leaves displaying their courtship behavior (Rossa-Feres et al. 2000). Additionally, adult and immature spiders use the base of the rosette as a refuge against predators (Romero and Vasconcellos-Neto 2005a; Omena and Romero 2008) and fire (G.Q. Romero and Omena, unpublished data).

General procedures

We collected individuals of *P. chapoda* from *B. balansae* in the surroundings of São José do Rio Preto city, São Paulo State. To perform the experiments we used only adult males and adult or subadult females. Spiders were transferred to the laboratory where they were kept individually with food *ad libitum* (*Drosophila melanogaster*) and with a piece of moist cotton in dram vials (15 cm high, 7 cm diameter) for 1-2 days. The laboratory was set under natural illumination and the temperature ranged from 24 to 34°C. The experiments were carried out in an open grassland space located on the experimental area of the Universidade Estadual Paulista. Spiders were transferred individually from laboratory to the experimental area inside transparent acrylic vials (5.5 cm high, 5.0 cm diameter). We used 30 males and 30 females for each of the visual selection experiments (i.e., experiments I, II and III); and 60 males and 60 females for the permanence time experiment. Each spider was tested only once. After performing the experiments we reintroduced all spiders in the same site where they were captured.

Experiment I: visual selection of diverse monocots and dicots

To investigate if *P. chapoda* visually recognizes and selects rosette shaped plants over others architectures, we used squared arenas containing four plant species, two of which were monocotyledons and the other two were eudicotyledons. One of the monocots has long leaves arranged in rosette (*Agave angustifolia*, Agavaceae), an exotic plant sharing similar morphological traits with Bromeliaceae; the other, *Euterpe oleracea* (Arecaceae) has long leaves, albeit without rosette formation. The eudicotyledons were *Croton floribundus* (Euphorbiaceae), which has long and wide leaves, and *Delonix regia* (Fabaceae) which has large leaves, but bears minute secondary leaflets (Figure 1, Table 1).

Each arena (n = 5) consisted of a square wooden board, with sides of 0.5 m, surrounded by four plants, one individual of each experimental plant species (i.e., *Ag. angustifolia*, *E. oleracea*, *C. fluribundus* and *D. regia*), which were placed in individual pots. For each trial, we arranged the plants randomly by drawing at the vertices of the square board. We used the pots edges to support the board, in a manner that the vegetative part of the plants were positioned above the boards, i.e., in the visual field of spiders, and the pot under the boards. We conducted the experiment between 10:00 h and 15:00 h, since *P. chapoda* lives in open area grasslands and withstand daily intense luminosity and high temperatures. For each replicate, we placed the acrylic vial containing one spider in the center of the arena, and then, we removed the lid from the vial to allow the spider to visualize and freely select the substratum. We took the observations on the spider behaviors from at least 3 m apart to avoid interference. A single spider was released upon each trial; we considered a choice if the spider jumped or climbed on a plant. In addition, we recorded the time spent by the spider to select the

plant. Before each trial, we rearranged the plants (i.e. in clockwise and sometimes in anticlockwise) and cleaned with a flannel the silk sign released on the board by the preceding.

Experiment II: visual selection of bromeliad traits

We also sought to verify whether *P. chapoda* visually recognizes and select its host plant (i.e., *B. balansae*) or bromeliads that share similar morphological traits with *B. balansae*. For this purpose, we used four bromeliad species (*B. balansae*, *Aechmea distichantha*, *Ae. blanchetiana* and *Ae. fasciata*) arranged in arenas as above. *Bromelia balansae* and *Ae. distichantha* have long and narrow leaves with margins covered with spines; however, the later differs in its leaf base, which has a lateral expansion that forms a phytotelmata (Table 1). *Aechmea blanchetiana* and *Ae. fasciata* also bears phytotelmata; the first has intermediate leaf length when compared to *B. balansae* and *A. fasciata*, but the former has leaf width as broad as *A. fasciata*. *Aechmea fasciata* posses the shortest leaves of these bromeliads (Figure 1, Table 1). We conducted this experiment using the same procedures described for the experiment I regarding arena configuration, number of plants and release of spiders.

Experiment III: visual detection of hosts on photos

In this experiment we aimed to verify if *P. chapoda* visually recognizes and selects its host plant or bromeliads that share similar architectural features with *B. balansae*, excluding the potential influence of plant colors and volatile chemical compounds released by the host plant. For this, we used photos of the four bromeliad species used in the second experiment (i.e., *B. balansae*, *Ae. distichantha*, *Ae. blanchetiana* and *Ae.*

fasciata). We presented the bromeliad photos in realistic sizes, and in black-and-white color to exclude any influence of color in plant choice. For this, we edited the photos with Adobe Photoshop CS3® to remove colors, remaining only the bromeliad image on a white background. To standardize photo paper size, we attached them on polystyrene boards of 80 cm in width x 60 cm in height. We fixed the polystyrene boards in wood stalks, which were used to fix the photos perpendicularly to the ground. We put the four photos on the edges of a square lumber board with sides of 80x80cm; the board was the arena's base and the photos formed four walls. Thus the experimental arena had the appearance of a box opened at the tip. Two persons realized the observation on the spider behaviors. For this they stayed on ladders of 1.5 m high which were 3 m apart of the arena to avoid interferences. For each replicate we changed the position of the photos (i.e. clockwise or anticlockwise) and removed the silk sing of the antecedent spider. We recorded the time that spiders took to select the photos and we also distinguish whether spiders jumped exactly on the bromeliad image or on the white background.

Experiment IV: permanence time of spiders on plants

To investigate if *P. chapoda* spiders are able to recognize a preferred host when experimentally placed on plants bearing distinct architectures, we compared the permanence time of *P. chapoda* among plants with distinct architectural traits. We run a randomized block experiment using six plant species per block; four were bromeliads (*B. balansae*, *Ae. distichantha*, *Ae. blanchetiana*, and *Ae. fasciata*) and the other two were eudicotyledons (*C. floribundus* and *D. regia*). We set up each block (n = 10) randomly in circles; each plant was 1 m apart from its nearest neighbors and each block

was at least 3 m apart from the next. We randomly selected the blocks to receive males or females, and each plant received only one spider. To determine the permanence time of spiders on plants we observed daily the experimental blocks between 7:30 to 20:00 h. At the beginning of each observation (i.e., 7:30 h) we inspected all plants to verify if all spiders were on their plants. If we detected that some spider was not on its plant we considered that the last time we saw it (i.e., 20:00 h of the day before) was the end of its permanence time on plant. All spiders were removed from the experimental area as soon as they left their hosts.

Statistical analyses

We compared the number of choices made by spiders on the experiments I, II and III using the G test for goodness-of-fit (Sokal and Rohlf 1995). For the second and third experiments pair-wise comparisons were conducted using G test, with required significance values adjusted using the sequential Bonferroni procedure (Rice 1989). *Psecas chapoda* colonizes more frequently rosette plants bearing long, but especially, narrow leaves than plants with other architectures (Omena and Romero 2008). Thus, to perform the pair-wise comparisons, we grouped bromeliads with similar architecture, in two categories: 1) plants that have narrow leaves (i.e., *B. balansae* and *Ae. distichantha*) and 2) plants that have broad leaves (i.e., *Ae. blanchetiana* and *Ae. fasciata*). For these analyses α values were adjusted to 0.025 by the Bonferroni correction. We compared the time in which males and females spent to choose plants (experiment I) using t-test for independent samples. A two-way analysis of variance (ANOVA) was used to compare the time spent by males and females to select hosts between the experiments II and III; sex and experiments were the fixed effect and time was the response variable. If

necessary, data were $\log_{10}(x+1)$ transformed for normalization and homogenization of variances (Sokal and Rohlf 1995). We performed Fisher LSD post hoc test to compare the time that males and females spent to choose bromeliads and photos of bromeliads and to compare this time between these experiments.

A randomized-block ANOVA was used to compare the permanence time of spiders on plants (Sokal and Rohlf 1995); blocks were the random effect, treatments (plants) and sex (male and female) were the fixed effect and the permanence time was the response variable. Prior to analysis, we verified the assumptions of ANOVA including all the six treatments. However, the distribution of residual variances was not normal and homogeneous, even after logarithmical transformation. To make possible the normalization and homogenization of residual variances we excluded data from the treatments *D. regia* and *C. floribundus*, in which spiders remained for the smallest period of time. We then performed *t*-test to compare the permanence time of males and females on bromeliads. During the experiment one female that was on an *Ae. blanchetiana* was preyed on by a *Pitangus sulphuratus* (Tyrannidae), therefore we excluded this block from the analysis.

Plant characterization

We performed a Discriminant Analysis (DA) to characterize the experimental plants and to show what traits best discriminate them. We carried out the analysis using some morphological parameters of plants, such as leaf or leaflet length (LL), leaf or leaflet width (LW), LW: LL ratio, leaf or leaflet number (LN) and distance between leaves or leaflets (LD) (Table I). Data were log10 transformed to meet normalization and equalization of variances.

The analysis classified about 96% of plant species (100% of *B. balansae*, 80% of *Ae. distichantha*, 100% of *Ae. blanchetiana*, 90% of *Ae. fasciata*, 100% of *Ag. angustifolia*, 100% of *E. oleracea*, 100% of *C. floribundus* and 100% of *D. regia*) (Figure 1). The most important parameter which discriminated plant groups was distance between leaf bases and leaf width (F-statistics: LD = 699.88, LW = 57.52, LW:LL = 26.07, LN = 32.12, LL = 28.59). The first canonical variable (factor 1) better discriminated the species (eigenvalue of factor 1 = 168.94; eigenvalue of factor 2 = 106.65). The architecture of plant species without rosette shape (i.e., *E. oleraceae*, *C. floribundus* and *D. regia*) differed from those bearing rosette architecture (Figure 1). Each one of those plant species formed a group distinct and distant from those of rosette shape species (Figure 1). Bromeliad species were separated in two groups, one of them contained *B. balansae* and *Ae. distichantha*, and the other *Ae. blanchetiana* and *Ae. fasciata*. The most important parameter that separated groups of bromeliads was leaf width, since the distance between its leaf bases was zero; the first group contained plants with narrow leaves and the later plants that have broad leaves (Table I). *Agave angustifolia* was similar to bromeliads, especially *Ae. distichantha* (Figure 1).

RESULTS

Experiment I.

Males and females of *P. chapoda* exhibited the same pattern of host plant selection. They selected preferentially *Ag. angustifolia* (females: $G = 65.71$, n = 30; df = 3, $P < 0.0001$; males: $G = 69.31$, n = 25; df = 3, $P < 0.0001$, Figure 2A). Males which did not select *Ag. angustifolia* (n = 5) displayed an escape behavior and did not select any of the available plants. The time that males and females spent to select their plants were

similar (mean time in seconds ± SE; males: 174 ± 35.19; females: 128 ± 29.81; $t = 1.01$; df = 28; $P = 0.321$).

Experiment II.

Females chose bromeliad species in a manner inconsistent with random chance ($G = 15.8$, n = 30; df = 3, $P < 0.001$, Figure 2B). The same occurred for males ($G = 21.58$, n = 30; df = 3, $P < 0.0001$, Figure 2B). Bromeliads bearing narrow leaves were more frequently selected by males ($G = 18.03$, n = 26, 4; df = 1, $P < 0.0001$, pair-wise comparisons) and females ($G = 8.99$, n = 23, 7; df = 1, $P = 0.0027$, pair-wise comparisons) indicating preference for *B. balansae* and *Ae. distichantha* in both sexes.

Experiment III.

Similar patterns of host plant selection found for living bromeliads were also obtained using bromeliad photos (Figure 3). Photos of bromeliads that have narrow leaves were selected more frequently by females ($G = 18.03$, n = 26, 4, df = 1, $P < 0.0001$, pair-wise comparisons) and males ($G = 8.99$, n = 23, 7, df = 1, $P = 0.0027$, pair-wise comparisons). Most of the females (87%) and males (88%) that chose bromeliads with narrow leaves first selected bromeliad images instead of white background (Figure 3).

Experiment II vs experiment III.

Time spiders spent to select bromeliads depended on the experiment (i.e., real bromeliads vs. bromeliad's photos) and sex (sex: $F_{1,116} = 8.02$, $P = 0.005$; experiment: $F_{1,116} = 47.46$, $P < 0.001$; sexes*experiments: $F_{1,116} = 4.23$, $P = 0.042$, two-way ANOVA). Both males and females spent less time to select real bromeliads than

bromeliad photos. The time that males and females spent to select real bromeliads did not differ ($t = 1.43$; df $= 55$; $P = 0.78$, Figure 4). In contrast, males chose bromeliad photos faster than females ($t = 2.44$; df $= 53$; $P = 0.017$, Figure 4).

During the experiments I, II and III we observed a behavioral pattern displayed by nearly all spiders when choosing its hosts. As soon as we removed the lid from the vials, at the center of arenas, the spiders climbed the vial's wall up to the rim, where they continuously kept walking for some seconds. During walking, they scanned the surroundings visualizing all available plants, as they stopped walking they jumped directly to their preferred plant. In the experiment IV, we observed males living their plants and moving towards the ones in which females were residents.

Experiment IV.

The time that females remained on plants differed among bromeliad species ($F_{3.24} = 9.27$; $P < 0.001$, one-way ANOVA, Figure 5). The permanence time of females on *B. balansae* and on *A. distichantha* did not differ ($P = 0.17$, Fisher LSD *pos-hoc* test), but was higher than on *A. blanchetiana* and *A. fasciata* ($P < 0.005$, Fisher LSD *pos-hoc* test). Time that females remained on *B. blanchetiana* and *A. fasciata* did not differ ($P = 0.06$, Fisher LSD *pos-hoc* test). Males also presented differences in the time they remained on plants ($F_{3,27} = 7.74$, $P = 0.0007$, one-way ANOVA, Figure 5). Permanence time of males on *B. balansae* was higher than on the other bromeliads ($P = 0.032$, Fisher LSD *pos-hoc* test). The time that males remained on *A. distichantha* did not differ from *A. blanchetiana* ($P = 0.19$, Fisher LSD *pos-hoc* test) but was higher than on *A. fasciata* ($P = 0.03$, Fisher LSD *pos-hoc* test). The permanence time of spiders on non-bromeliad plants (i.e., *D. regia* and *C. floribundus*) was almost zero (mean in hours

± SE: males: 0.04 ± 0.01; females: 0.03 ± 0.008, Figure 5). Females remained on average 23.5 times longer on bromeliads than males (t = 4.76, df = 73, P < 0.001, Figure 5).

DISCUSSION

Our findings show that *Psecas chapoda* selects their preferred substrata by evaluating architectural features of leaves and rosette of the host plants, and that the underlying basis of these choices is governed by visual stimuli. Jumping spider's vision is typically based on exceptionally high spatial acuity (Land 1969a, b; Blest, O'Carrol, and Carter 1990; Clark and Uetz 1990; Land and Fernald 1992), a trait that may confer to *P. chapoda* a high ability to find its host plant. The host *B. balansae* is a suitable site for this spider species, as have been reported elsewhere (see Romero and Vasconcellos-Neto 2005a; Romero 2006; Omena and Romero 2008). Moreover, it is a very abundant and has a conspicuous architecture that differs from others in the landscape. In addition, it is a resource occurring widely throughout several places in South America (Romero 2006). Thus, it is a reliable source of visual information that may be explored by the spiders to find their host. Besides that, a well-developed visual acuity may be of crucial importance for this salticid, since individuals probably migrate among bromeliads to obtain food resources, mate opportunities and shelter. Because these spiders are more vulnerable to predators when they are outside their hosts (PM Omena, personal observation), an inefficient ability to quickly detect their plants could be translated into increased mortality risk.

Both males and females detected visually and selected its bromeliad host plant (*B. balansae*), as well as bromeliads that share similar traits with this host plant (e.g.,

Ae. distichantha) or even non-bromeliad plants but which bear rosette architecture (i.e., *Ag. angustifolia*). These results confirmed our hypothesis that host plant selection is based on microhabitat architecture instead of plant taxonomy (Omena and Romero 2008). Romero and Vasconcellos-Neto (2005a) proposed that *P. chapoda* spiders have a high efficiency in finding their host plants, and that they are capable of recognize and evaluate, in fine details, the physical features of microhabitat. In our results, we found that this salticid was able to distinguish specific architectural features of rosette-shaped plants. Guided by visual stimuli these spiders recognized and selected bromeliads bearing both narrow and long leaves (i.e., *B. balansae* and *Ae. distichantha*). The great ability in detecting differences in plants architecture possibly reflects an adaptation of this salticid to encounter, in an efficient manner, microhabitats that are favorable to spider survivorship (see Romero and Vasconcellos-Neto 2005a; Romero 2006; Omena and Romero 2008). The scanning behavior displayed by *P. chapoda* when choosing their host is another evidence of such high ability to detect hosts. Some authors have reported that the vision of jumping spiders allow them to examine the environment before starting a route (Tarsitano and Jackson 1997; Tarsitano 2006). *Psecas chapoda* scanned and evaluated its surroundings (in experimental arenas) before moving towards the host plants. The capacity of salticids in evaluating the environment likely favored evolution of this unusual spider-plant association; since, the acute vision of *P. chapoda* associated with the large availability of a substratum (i.e. *B. balansae*) may have favored the evolution of such mutualistic system (see Romero et al. 2006).

Psecas chapoda was able to choose its preferred host plants (i.e., *B. balansae* and *Ae. distichantha*) even on black-and-white photos. This result suggests that visual cues are the most important sense used by this salticid to select its preferred

microhabitat. The ability of *P. chapoda* in recognizing host plant photos indicate that plant chemical volatiles are not used as cues by this spider to find its hosts. Other spiders were also reported using visual stimuli to encounter their hosts (e.g., Heiling et al. 2005). Despite some studies have reported spiders selecting plants based on substrata color (Greco and Kevan 1994; Heiling et al. 2005), to our knowledge, this is the first one to experimentally demonstrate visual detection of host plant architecture by spiders.

Although males and females of *P. chapoda* chose bromeliads and photos of bromeliads following the same pattern of host plant selection, they spent more time to choose photos. Some authors have reported that jumping spiders could discriminate colors, being apparent that salticids have some form of true color vision (Nakamura and Yamashita 2000). Many jumping spiders have green cells in their principal eyes (DeVoe 1975; Yamashita and Tateda 1976; Blest et al. 1981; Nakamura and Yamashita 2000). Thus, it is possible that the color of bromeliads (i.e., green) could play some influence on microhabitat selection by *P. chapoda*, facilitating somehow the encounter of plants by spiders. Notwithstanding, even using black-and-white photos, spiders were able to identify their preferred architecture. Additionally, the majority of these individuals jumped exactly on the bromeliad image and lesser on the white background reinforcing the evidence that spiders truly recognize leaf structures. In that manner, if color has some influence in host plant selection, this influence probably play a secondary role, being the architecture *per se* the most important parameter used to evaluate plants. In addition, the pictures lack the bromeliad tridimensionality; this could also have played some influence in the time spent by spider to recognize and select their hosts.

Individuals of *P. chapoda*, once on a plant, can identify whether or not they are on a preferred substratum. The permanence time of females was expressively higher on

bromeliads with narrow and long leaves (i.e. *B. balansae* and *Ae. distichantha*) than on other experimental plants. These spiders likely identify visually the structure of leaves and rosette even when inside rosettes, but may also use tactile cues to evaluate the structure of leaves (i.e. leaf texture and width). In spite of the fact that males stayed longer on *B. balansae* but not distinguish between *A. distichantha* and *A. blanchetiana*, they did not remain much longer in any of the experimental plants. Kotiaho et al. (1998) reported that males of *Hygrolycosa rubrofasciata* (Lycosidae), in the field, are much more mobile than females. While females do not move much, males have to move more to increase the probability of encountering a receptive female. *Psecas chapoda* exhibits a similar pattern of activity, since females tended to remain on their preferred bromeliads for a period of time higher than males. Besides that, we observed males moving from their hosts in direction to bromeliads (i.e. *B. balansae* and *Ae. distichantha*) in which females were resident.

We did not find differences in the time that males and females spent to select the real bromeliads. However, males selected photos of bromeliads faster than females. This might be an indicative that males recognize architecture of bromeliads more promptly than females. The recognition of host plants by males probably is crucial for their survival and fitness, since *P. chapoda* spiders are more vulnerable to predator attempts when outside their hosts (PM Omena, personal observation). In addition, the only spiders seen outside the bromeliads (on other vegetation or ground) were adult males (n = 3; GQ Romero, personal observations), indicating that males are likely the more vulnerable sex. Studies that have examined mate-searching costs show that predation rates can be high and that mortality is often biased toward the sex that does the searching (Gwynne 1987; Gwynne and Bussière 2002; Kasumovic et al. 2006). Thus,

the survivor and fitness of *P. chapoda* males depends on their ability to efficiently detect host plants with receptive female residents.

To our knowledge, this is the first study to demonstrate the mechanisms involved in detection and selection of host plants by Salticidae spiders. Guided by visual stimuli, *P. chapoda* can evaluate and distinguish physical structure of microhabitats and actively select its hosts. In a broad scale, the microhabitat specialization of *P. chapoda* is restricted to rosette shaped plants; in smaller scale, this spider selects preferentially those plants in which leaves are both narrow and long. Although males and females present the same pattern of host plant selection, males apparently are able to detect architectural features of their hosts faster than females. This is likely an adaptation against the higher vulnerability of males to predation caused by the mate searching behavior. This spider-plant association likely evolved because the host plant *B. balansae* is abundant and widespread over a large geographic region, and because the great visual acuity of *P. chapoda* enables it to find home in an efficient manner.

REFERENCES

Aldrich JD, Barros TM. 1995. Chemical attraction of male crab spiders (Araneae, Thomisidae) and cleptoparasitic flies (Diptera, Milichiidae, and Chloropidae). J Arachnol. 23:212-214.

Blest AD, Hardie RC, McIntyre P, Williams DS. 1981. The spectral sensitivities of identified receptors and the function of retinal tiering in the principal eyes of a jumping spider. J Comp Physiol A. 145:227–239.

Blest AD, O'Carrol DC, Carter M. 1990. Comparative ultrastructure of Layer I receptor mosaics in principal eyes of jumping spiders: the evolution of regular arrays of light guides. Cell Tissue Res. 262:445–460.

Clark DL, Uetz GW. 1990. Video image recognition by the jumping spider, *Maevia inclemens* (Araneae: Salticidae). Anim Behav. 40:884–890.

DeVoe RD. 1975. Ultraviolet and green receptors in principal eyes of jumping spiders. J Gen Physiol. 66:193–207.

Dias SC, Brescovit AD. 2003. Notes on the behavior of *Pachistopelma rufonigrum* Pocock (Araneae, Theraphosidae, Aviculariinae). Rev Bras Zool. 20:13–17.

Greco CF, Kevan PG. 1994. Contrasting patch choosing by anthophilous ambush predators: vegetation and floral cues for decisions by a crab spider (*Misumena vatia*) and males and females of an ambush bug (*Phymata americana*). Can J Zoolog. 72:1583–1588.

Gwynne DT, Bussière L. 2002. Female mating swarms increase predation risk in a 'role-reversed' dance fly (Diptera: Empididae: *Rhamphomyia longicauda* Loew). Behaviour. 139:1425–1430.

Gunnarsson B. 1996. Bird predation and vegetation structure affecting spruce-living arthropods in a temperate forest. J Anim Ecol. 65:389–397.

Halaj J, Ross DW, Moldenke AR. 2000. Importance of habitat structure on the arthropod food-web in Douglas-fir canopies. Oikos. 90:139–152.

Hill DE. 1979. Orientation by jumping spiders of the genus *Phidippus* (Araneae: Salticidae) during the pursuit of prey. Behav Ecol Sociobiol. 5:301–322.

Heiling AM, Cheng K, Herberstein ME. 2004. Exploitation of floral signals by crab spiders (*Thomisus spectabilis*, Thomisidae). Behav Ecol. 2: 321–326.

Heiling AM, Chittka L, Cheng K, Herberstein ME. 2005. Colouration in crab spider: substrate choice and prey attraction. J Exp Biol. 208:1785–1792.

Jackson RR. 1992. Eight-legged tricksters. BioScience 42:590–598.

Jackson RR, Pollard SD. 1996. Predatory behaviour of jumping spiders. Annu Rev Entomol. 41:287–308.

Kasumovic MM, Bruce MJ, Herberstein ME, Andrade MCB. 2006. Risky mate search and mate preference in the golden orb-web spider (*Nephila plumipes*). Behav Ecol. 18:189-195.

Krell FT, Krämer F. 1998. Chemical attraction of crab spiders (Araneae, Thomisidae) to a flower fragrance component. J Arachnol. 26:117–119.

Kotiaho J, Alatalo RV, Mappes J, Parri S, Rivero A. 1998. Male mating success and risk of predation in a wolf spider: a balance between sexual and natural selection? J Anim Ecol. 67:287–291.

Jackson RR. 1977. An Analysis of Alternative Mating Tactics of the Jumping Spider *Phidippus johnsoni* (Araneae, Salticidae). J Arachnol. 5:185–230.

Land MF. 1969a. Structure of the retinae of the principal eye of jumping spiders (Salticidae: Dendryphantinae) in relation to visual optics. J Exp Biol. 51:443–470.

Land MF. 1969b. Movements of the retinae of jumping spiders (Salticidae: Dendryphantinae) in response to visual stimuli. J Exp Biol. 51:471–493.

Land MF, Fernald RD. 1992. The evolution of eyes. Annu Rev Neurosci. 15:1–29.

Li D, Yik SH, Seah WK. 2002. Rivet-like nest-building and agonistic behaviour of *Thiania bhamoensis*, an iridescent jumping spider (Araneae: Salticidae) from Singapore. Raffles Bull Zool. 50:143–151.

Li D, Lim MLM. 2005. Ultraviolet cues affect the foraging behaviour of jumping spiders. Anim Behav. 70:771–776.

Lim MLM, Li D. 2006. Extreme ultraviolet sexual dimorphism in jumping spiders (Araneae: Salticidae). Biol J Linn Soc. 89:397–406.

Lim MLM, Land MF, Li D. 2007. Sex-specific UV and fluorescence signals in jumping spiders. Science. 315:481p.

Morse DH. 1988. Relationship between crab spiders *Misumena vatia* nesting success and earlier patch-choice decisions. Ecology. 69:1970–1973.

Morse DH. 2007. Predator upon a flower: life history and fitness in a crab spider. Cambridge, UK: Harvard University Press.

Nakamura T, Yamashita S. 2000. Learning and discrimination of colored papers in jumping spiders (Araneae, Salticidae). J Comp Physiol A. 186:897–901.

Omena PM, Romero GQ. 2008. Fine-scale microhabitat selection in a bromeliad-dwelling jumping spider (Salticidae). Biol J Linn Soc. 94:653–662.

Orians GH, Wittenberger JF. 1991. Spatial and temporal scales in habitat selection. Am Nat. 137:29–49.

Pulliam HR, Danielson BJ. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. Am Nat. 137:50–66.

Rice WR. 1989. Analyzing tables of statistical test. Evolution. 43:223–225.

Romero GQ. 2006. Geographic range, habitats and host plants of bromeliad-living jumping spiders (Salticidae). Biotropica. 38:522–530.

Romero GQ, Mazzafera P, Vasconcellos-Neto J, Trivelin PCO. 2006. Bromeliad-living spiders improve host plant nutrition and growth. Ecology. 87:803–808.

Romero GQ, Vasconcellos-Neto J. 2004. Spatial distribution patterns of jumping spiders associated with terrestrial bromeliads. Biotropica. 36:596–601.

Romero GQ, Vasconcellos-Neto J. 2005a. The effects of plant structure on the spatial and microspatial distribution of a bromeliad-living jumping spider (Salticidae). J Anim Ecol. 74:12–21.

Romero GQ, Vasconcellos-Neto J. 2005b. Population dynamics, age, structure and sex ratio of the bromeliad-dwelling jumping spider, *Psecas chapoda* (Salticidae). J Nat Hist. 39:153–163.

Romero GQ, Vasconcellos-Neto J. 2005c. Spatial distribution and microhabitat preference of *Psecas chapoda* (Peckham and Peckham) (Araneae, Salticidae). J Arachnol. 33:124–134.

Romero GQ, Souza JC, Vasconcellos-Neto. 2008. Anti-herbivore protection by mutualistic spiders and the role of plant glandular trichomes. Ecology. 89:3105–3115.

Rossa-Feres D de C, Romero GQ, Gonçalves-de-Freitas E, Feres RJF. 2000. Reproductive behavior and seasonal occurrence of *Psecas viridipurpureus* (Salticidae, Araneae). Braz J Biol. 60:221–228.

Sokal RR, Rohlf FJ. 1995. Biometry: the principles and practice of statistics in biological research. 3rd ed. New York, USA: W. H. Freeman and Company.

Tarsitano MS. 2006. Route selection by a jumping spider (*Portia labiata*) during the locomotory phase of a detour. Anim Behav. 72:1437–1442.

Tarsitano MS, Jackson RR. 1997. Jumping spiders chose between detour routes that do and do not lead to prey. Anim Behav. 53:257–266.

Tarsitano MS, Andrew R. 1999. Scanning and route selection in the jumping spider *Portia labiata*. Anim Behav. 58:255–265.

Tarsitano MS, Jackson RR, Kirchner WH. 2000. Signals and signal choices made by the araneophagic jumping spider *Portia fimbriata* while hunting the orb-weaving spiders *Zygiella x-notata* and *Zosis geniculatus*. Ethology. 106:595–615.

Vasconcellos-Neto J, Romero GQ, Santos A, Dippenaar-Schoeman AS. 2007. Associations of spiders of the genus *Peucetia* (Oxyopidae) with plants bearing glandular hairs. Biotropica. 39:221–226.

Vieira C, Romero GQ. 2008. Maternal care in a neotropical jumping spider (Salticidae). J Zool. 276:237-241.

Yamashita S, Tateda H. 1976. Spectral sensitivities of jumping spider eyes. J Comp Physiol A. 105:29–41.

Figure legends

Figure 1 Relationship between scores of factors 1 and 2 for the Discriminant Analysis of plant traits.

Figure 2 Percentage of active choices of non-bromeliad plants experiment I (A) and of bromeliad species experiment II (B) by *P. chapoda*. Significance level for pair-wise comparison with the *G* –test are show above the horizontal bars (ns = non significant; *** $P < 0.0001$). (A) Males: n = 25; females: n = 30, (B) males: n = 30; females = 30.

Figure 3 Percentage of active choices of bromeliad photos by females (A) and males (B) of *Psecas chapoda*. Different bands in the bars indicate the percentages of individuals that moved and firstly entered in contact with the bromeliad image or with the white background. Bars representing males and females are indicated by the symbols ♂ and ♀ respectively. Significance level for pair-wise comparison are shown above bars (ns = non significant; *** $P < 0.0001$). Males (n = 30) and females (n = 30).

Figure 4 Mean time (s) spent by males and females of *P. chapoda* to select bromeliads and photos of bromeliads. Bars indicate the standard error. Significance level for two-way ANOVA and for Fisher LSD *post-hoc* test is shown above bars (ns = non significant; *** $P < 0.001$; ** $P < 0.05$).

Figure 5 Mean permanence time (h) spent by females (n = 50) and males (n = 60) of *P. chapoda* on experimental plants. Bars indicate standard error.

Table I. Mean (± 1 SE) of leaf or leaflet length (LL) and width (LW), LW:LL ratio, leaf

or leaflet number (LN), distance between leaves or leaflets (DL), number of plants (N),

rosette (R) [present (P) or absent(A)] of the plant species used in the experiments.

| Plants	LL (cm)	LW (cm)	LN	LW:LL	DL (cm)	N	R
B. balansae	70.45±4.05	2.67±0.08	18.7±1.32	0.038±0.001	0	10	P
Ae. distichantha	50.75±3.28	2.21±0.09	31.1±2.46	0.045±0.003	0	10	P
Ae. blanchetiana	40.20±1.55	7.67±0.22	15.6±1.36	0.175±0.008	0	10	P
Ae. Fasciata	28.7±2.24	8.26±0.38	16.6±1.38	0.310±0.038	0	10	P
Ag. angustifolia	28.7±2.24	3.29±0.15	30.3±3.17	0.121±0.006	0	10	P
E. oleracea	30±1.84	5.65±0.56	6.3±0.39	0.20±0.025	19.65±1.2	10	A
C. floribundus	12.15±0.54	6.31±0.23	15.1±0.58	0.524±0.118	1.9±0.14	10	A
D. regia	1.17±0.07	0.63±0.03	2348.8±221.55	0.54±0.015	0.43±0.04	10	A
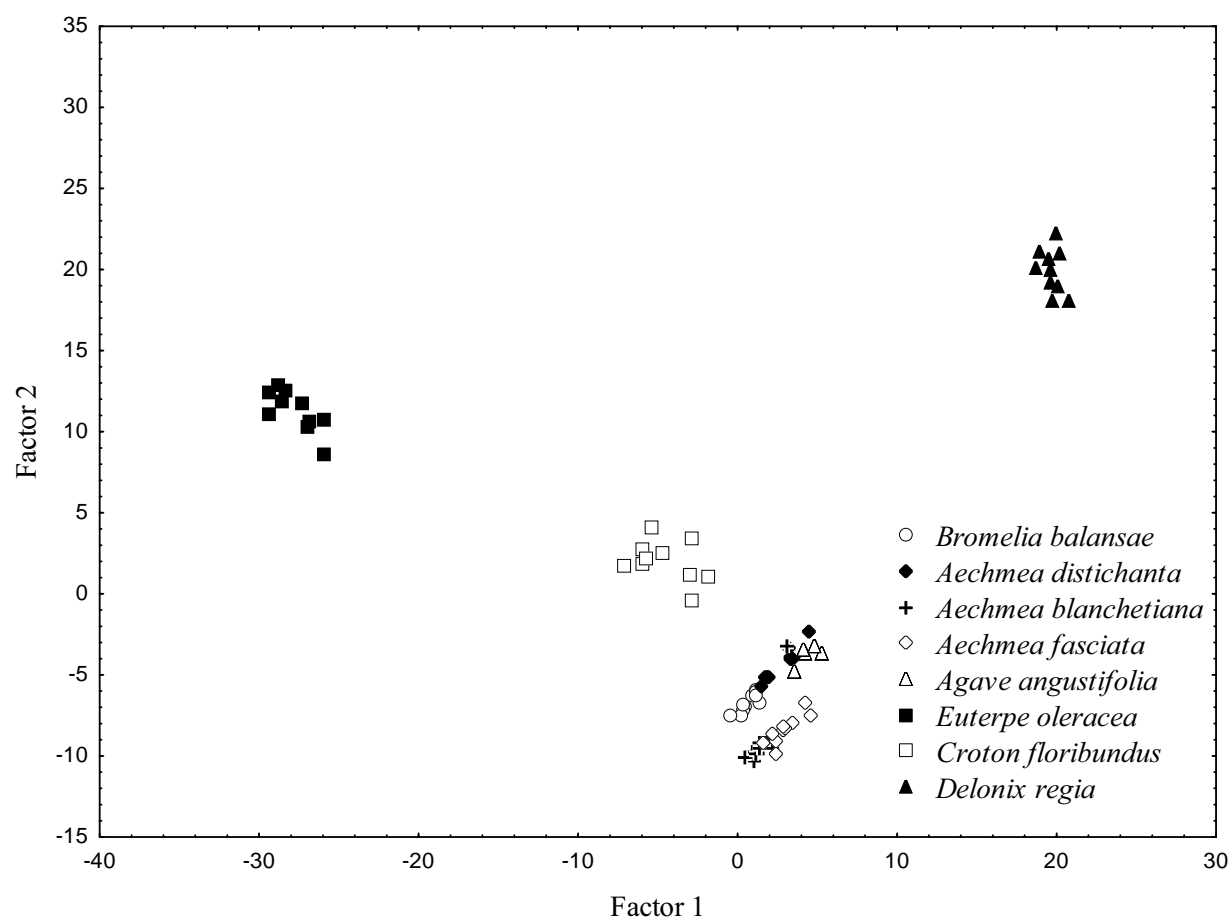
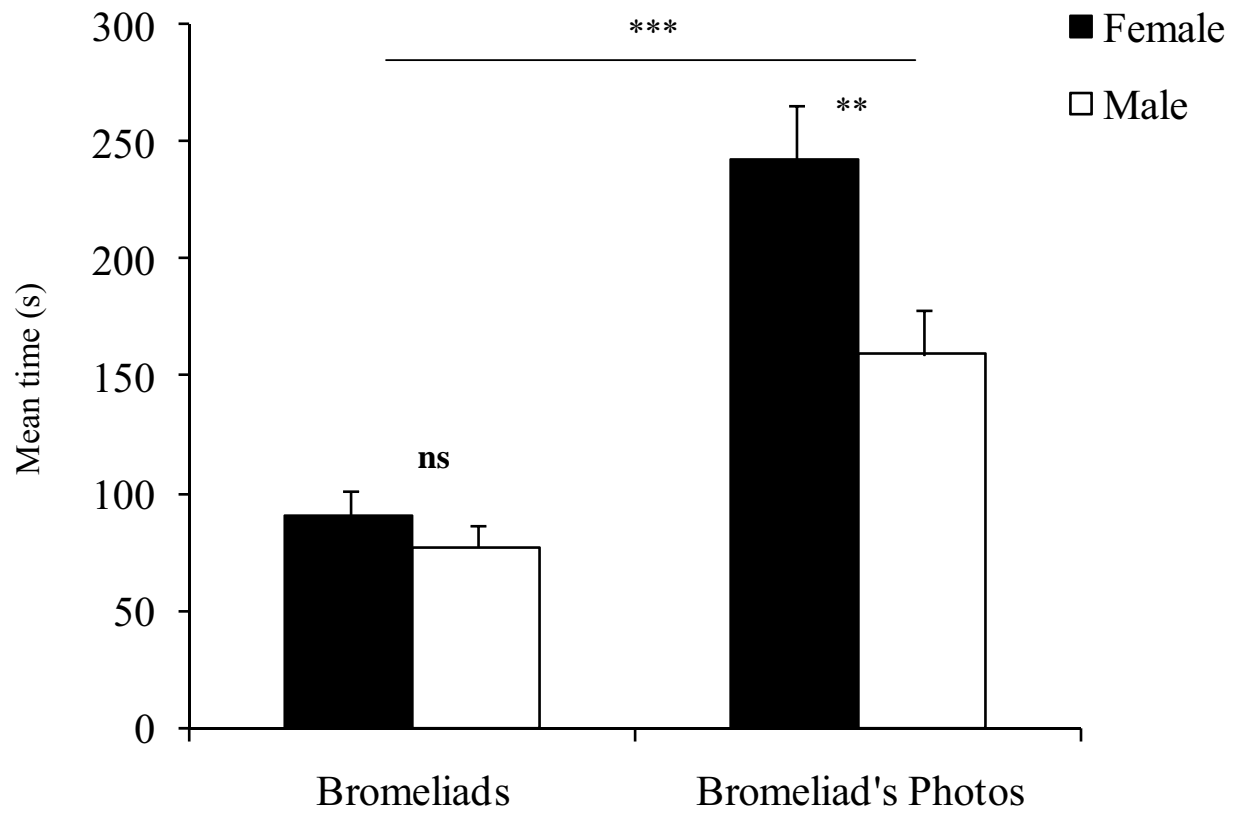**Figure 1**
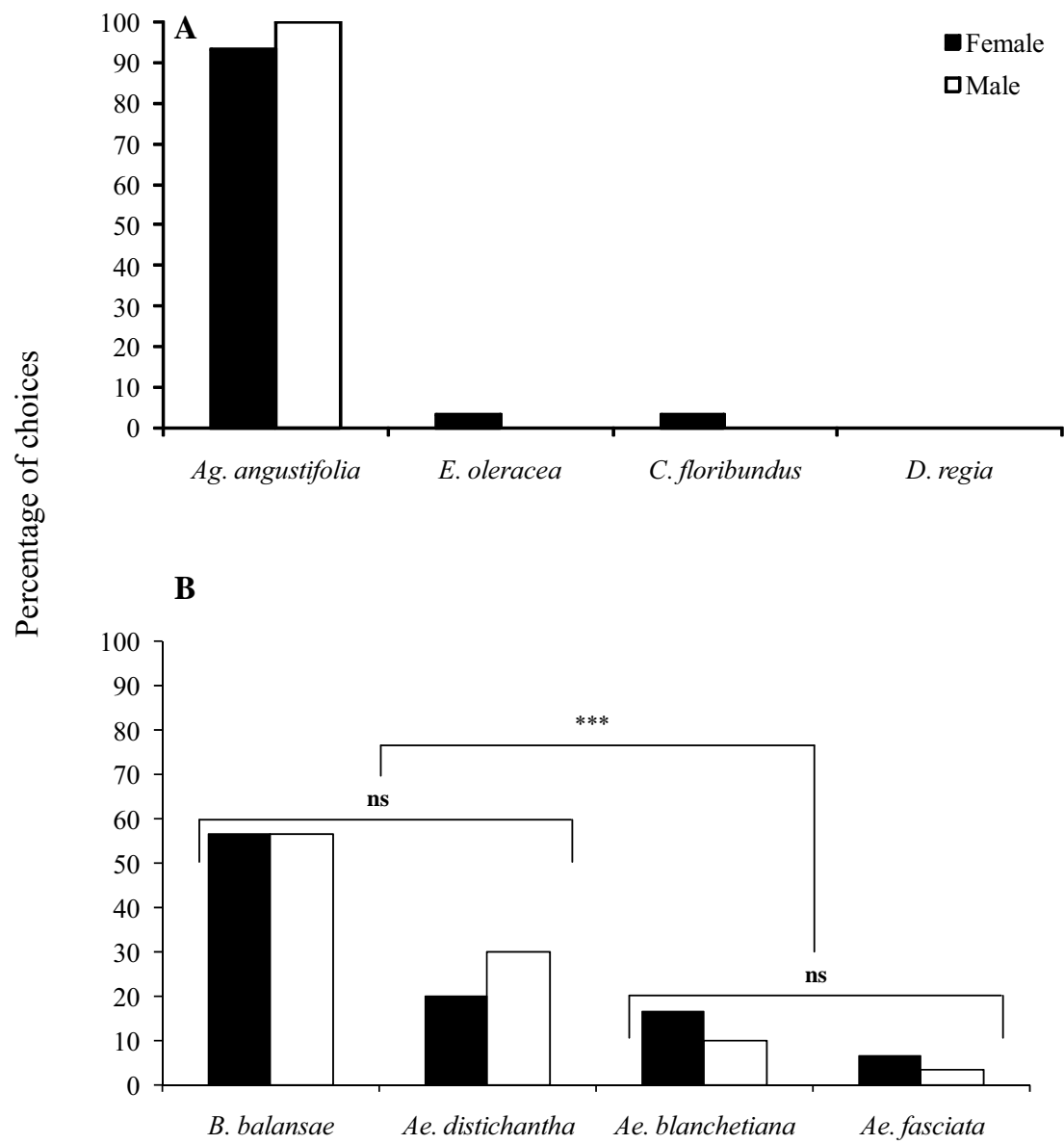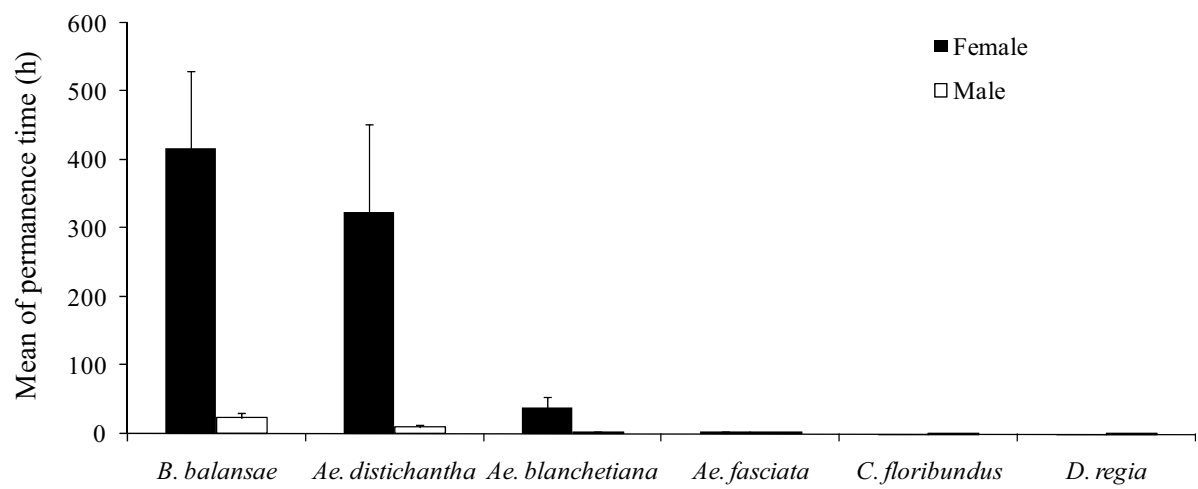
Figure 2
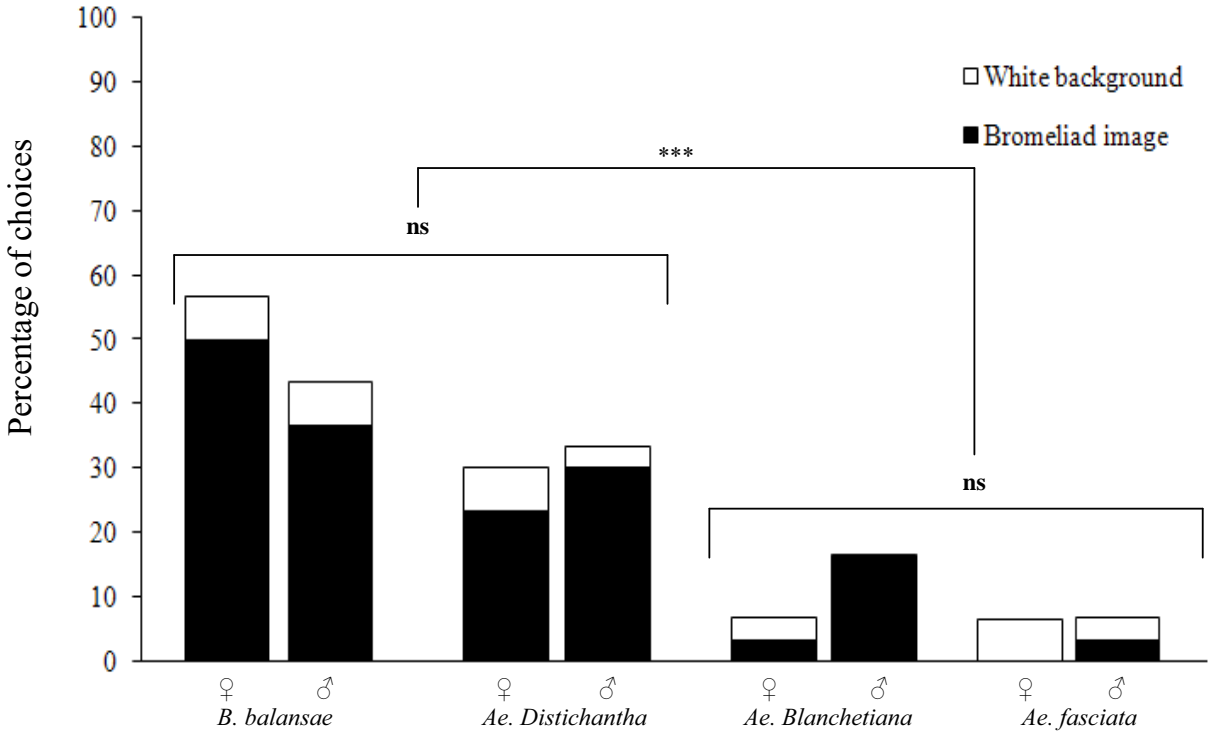
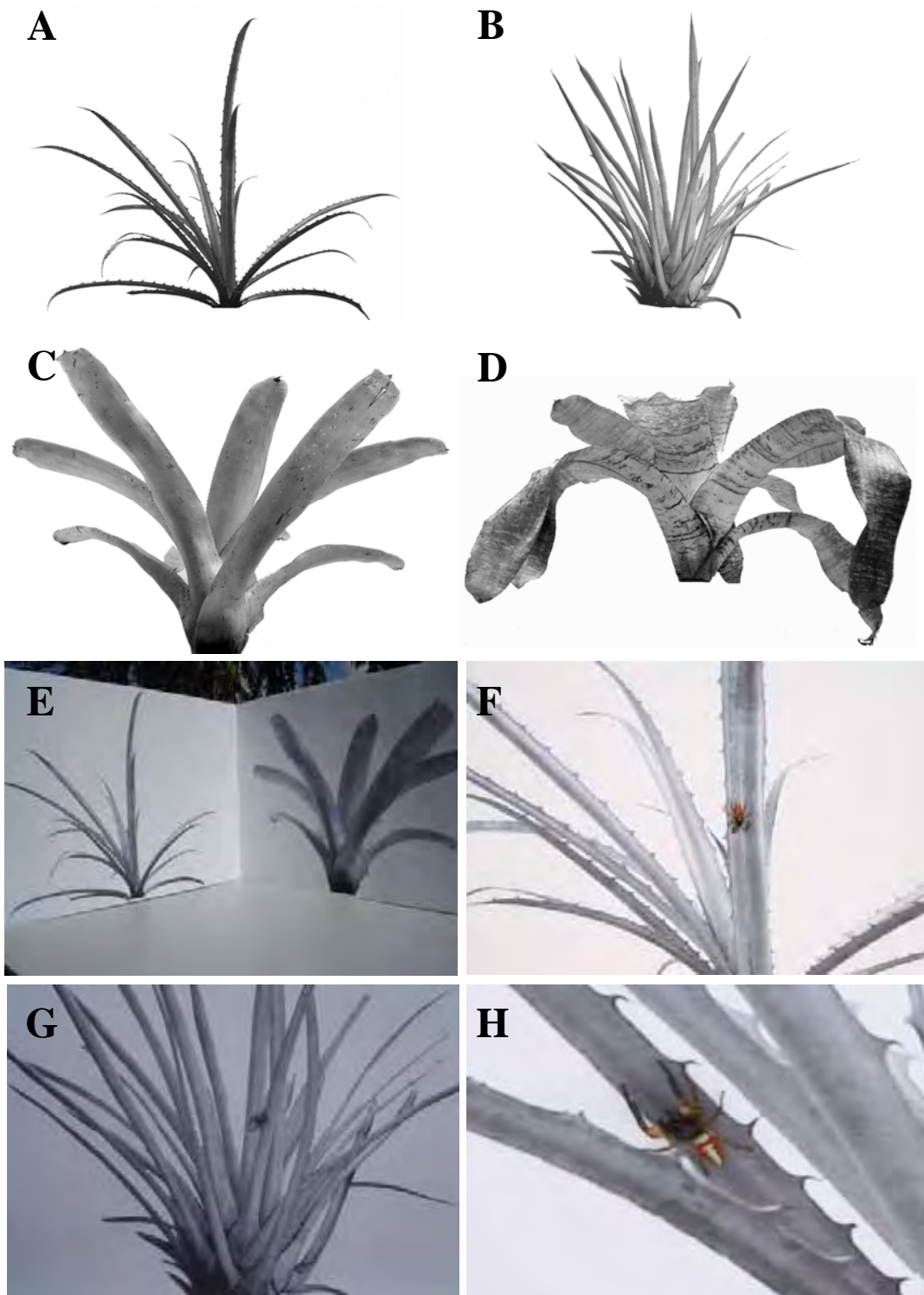**Figure 3**

Figure 4

Figure 5

Appendix

Figure 1. Photos of bromeliads used in the experiment III: *Bromelia balansae* (A), *Aechmea distichantha* (B), *Aechmea blanchetiana* (C) and *Aechmea fasciata* (D). View from the center of the experimental arena with the plants *B. balansae* and *Ae. blanchetiana* (E); female of *P. chapoda* on *B. balansae* photo (F); male of *P. chapoda* on *Ae. distichantha* picture; and detail of a female on *B. balansae* photo picture.

Neste trabalho realizamos experimentos em campo para testar a preferência de *Psecas chapoda* (i.e., taxas diferenciais de colonização) por diferentes espécies/arquiteturas de Bromeliaceae introduzidas nas áreas de estudo. Com estes experimentos pudemos sugerir que a especialização de micro-hábitat por *P. chapoda* não é espécie-específica e sim restrita a certas características arquiteturais das rosetas de suas plantas hospedeiras. Tais aranhas aparentemente utilizam a largura e o comprimento das folhas como pistas para avaliação e seleção de micro-hábitats. Também, pudemos inferir que a presença de fitotelmata e espinhos foliares não influenciavam a escolha do substrato por *P. chapoda*. Ainda, testamos se aranhas adultas da espécie *P. chapoda* escolhiam ativamente suas plantas hospedeiras, com base em dois tipos de experimentos (a) escolha visual em arenas experimentais contendo plantas com diferentes tipos de arquitetura e (b) tempo de permanência de aranhas introduzidas nas plantas com diferentes tipos de arquitetura. Os resultados deste experimento reforçaram as hipóteses aventadas no primeiro capítulo, e pudemos então, comprovar que *P. chapoda* guiada por estímulos visuais avalia e distingue estruturas físicas de micro-hábitats e seleciona ativamente suas plantas hospedeiras.

Machos e fêmeas apresentaram o mesmo padrão de seleção de plantas hospedeiras, no entanto, machos aparentemente são capazes de detectar a arquitetura *per se* de suas plantas mais rapidamente do que as fêmeas. Possivelmente, isto reflita uma adaptação a maior vulnerabilidade dos machos à predação ocasionada pelo comportamento de busca por fêmeas receptivas. Os resultados do experimento de tempo de permanência mostraram que as fêmeas tendem a não se deslocar muito, permanecendo por longos períodos em uma única planta hospedeira. Em contrapartida, o tempo de permanência de machos sobre as plantas é bem reduzido. Provavelmente machos deslocam-se mais para aumentar suas probabilidades de encontros com fêmeas receptivas aumentando assim, seu sucesso reprodutivo.

O padrão acima descrito é completamente incomum entre predadores invertebrados, e, provavelmente, evoluiu em virtude da grande abundância de um tipo específico de micro-hábitat aliado a excelente acuidade visual de *P. chapoda* (característica dos Salticidae) que possibilita a detecção eficiente de suas plantas hospedeiras. Além destes fatores, existem também os benefícios que este micro-hábitat oferece às aranhas, e.g., sítio de forrageamento, acasalamento e de postura de ootecas, bem como abrigo contra predadores e berçários.