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ASSOCIAÇÕES ENTRE ARANHAS SALTICIDAE E BROMELIACEAE:

HISTÓRIA NATURAL, DISTRIBUIÇÃO ESPACIAL E MUTUALISMOS

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Dedico este trabalho
à Lilian e Carolina,
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ABSTRACT

The understanding of the interactions between arthropods and plants has grown considerably in the last few years. Although the spiders are among the most abundant arthropod group and compose the main predator guild on vegetation, there exist very few studies involving spiders and plants. Here, we report information showing that some salticid species are strictly associated with the Bromeliaceae in several South American phytophysiognomies, including cerrados (savanna-like vegetation), semideciduous and seasonal forests, coastal sand dune vegetation, restingas, inselbergs, highland forests, chacos and rain forests in several localities of Brazil, Paraguay, Bolivia and Argentina. While some species are specialists, occurring almost exclusively on a single host plant species (e.g., *Psecas chapoda* on *Bromelia balansae*), others are generalists and inhabit up to 7-8 bromeliad species. Generally, the spiders inhabited the larger bromeliads and/or those with natural architecture (e.g., simulation of inflorescence or inclusion of dry leaves in the center of the rosette). Therefore, the spiders seem to evaluate, in fine detail, the physical state of their microhabitats. Bromeliads may often provide specifically suitable microhabitats for jumping spiders. Their leaves form a complex tri-dimensional architecture (rosette), which can be used by adults and immature as shelter against predators or harsh climatic conditions, as foraging, mating and laying egg sites, and as nursery for spiderlings. In exchange, the spiders contributed to bromeliad nutrition. By using stable isotope methods (^{15}N), we found that *P. chapoda* contributed with up to 40% of the total nitrogen of *B. balansae* in the field. However, the beneficial effects of the spiders were weakened where they occurred in low abundance, and conditionality was generated by spatial variation in spider density.

RESUMO

O entendimento das interações entre artrópodes e plantas tem crescido consideravelmente nos últimos poucos anos. Embora as aranhas estejam entre os grupos de artrópodes mais abundantes e constituam as principais guildas de predadores sobre a vegetação, poucos estudos envolvendo aranhas e plantas foram desenvolvidos. Aqui, reportamos um conjunto de informações mostrando que algumas espécies de salticídeos são estritamente associadas com Bromeliaceae em várias fitofisionomias sul-americanas, incluindo cerrados, florestas semidecíduas e sazonais, vegetação de dunas costeiras, restingas, afloramentos rochosos, florestas de altitude, chacos e florestas ombrófilas densas, em várias localidades do Brasil, Paraguai, Bolívia e Argentina. Enquanto algumas espécies de aranhas foram especialistas, ocorrendo quase exclusivamente em uma única espécie de planta hospedeira (e.g., *Psecas chapoda* sobre *Bromelia balansae*), outras foram generalistas e habitaram até 7-8 espécies de bromélias. Geralmente, as aranhas habitaram e selecionaram as bromélias maiores e/ou aquelas com arquitetura natural (e.g., simulação de inflorescência ou inclusão de folhas secas no centro da roseta). Portanto, as aranhas podem avaliar, em detalhes finos, o estado físico dos seus microhabitats. Bromélias podem muitas vezes fornecer microhabitats apropriados específicos para salticídeos. Suas folhas formam uma arquitetura tridimensional complexa (roseta), que pode ser usada por adultos e imaturos como abrigo contra predadores ou condições climáticas severas, como sítios de forrageamento, acasalamento e de oviposição, e como berçários para as recém emergidas das ootecas. Em troca, as aranhas contribuíram para a nutrição das bromélias. Usando métodos isotópicos (^{15}N), nós verificamos que *P. chapoda* contribuiu com até 40% do N total de *B. balansae* no campo. Entretanto, os efeitos benéficos das aranhas foram enfraquecidos onde estas ocorreram em baixa abundância, e a condicionalidade foi gerada pela variação especial na densidade de aranhas.

1. INTRODUÇÃO

Interações envolvendo aranhas e plantas

Aranhas estão entre os animais mais comuns nos ambientes terrestres. Ocupam os mais diversos habitats, desde os desertos mais áridos e quentes até as cavernas mais profundas e as montanhas mais altas e frias. Muitas se dispersam pelo vento e podem alcançar elevadas altitudes no espaço aéreo (Turnbull 1973, Suter 1999). As aranhas apresentam grande variedade de estilos de vida, comportamentos e adaptações morfológicas e fisiológicas (Foelix 1982). Ocupam a sétima posição no ranking dos grupos animais mais ricos em espécies na Terra, com 38.834 espécies descritas (Coddington & Levi 1991, Platnick 2005).

Uma vez que as aranhas são predadores obrigatórios, podem afetar profundamente a dinâmica das populações, como também a estrutura das comunidades das suas presas (Wise 1993). Além disso, insetos herbívoros são freqüentemente incluídos na sua dieta, podendo resultar em um notório decréscimo das taxas de herbivoria das plantas onde ocorrem (revisão em Romero & Vasconcellos-Neto 2005a). De fato, um considerável número de estudos ecológicos aplicados tem apontado as aranhas como excelentes agentes de controle biológico de pragas nos agroecossistemas (revisão em Romero 2005). Apesar das aranhas estarem entre os artrópodes mais abundantes e diversos na vegetação, relativamente poucos estudos são direcionados a compreender suas interações com plantas, especialmente se habitam exclusivamente plantas com traços morfológicos específicos e se mantém associações mutualísticas com suas plantas hospedeiras. Estudos examinando interações aranha-planta têm seguido rotas diferentes e com integração limitada de efeitos mutualísticos para ambos parceiros. Por um lado, aranhas são freqüentemente usadas como modelos de predadores para responder questões relacionadas às dinâmicas e estruturas de cadeias alimentares (revisão em Romero & Vasconcellos-Neto 2005a). Por outro lado, estudos vêm debatendo como aspectos morfológicos e estruturais das plantas beneficiam aranhas e como mudanças na arquitetura das plantas afetam a composição e distribuição das aranhas. Um outro conjunto de estudos tem ainda reportado que aranhas recebem benefícios das plantas pela obtenção de recursos alimentares alternativos, como néctar e pólen.

Nesta revisão, forneço evidências recentes de interações mutualísticas facultativas entre aranhas e plantas. Várias espécies de aranhas vivem exclusivamente associadas a plantas com determinados tipos de arquitetura e são beneficiadas de várias formas com esta associação. Em retorno, as aranhas podem remover herbívoros e até mesmo nutrir suas plantas hospedeiras com fezes e carcaças de presas.

Principais famílias e guildas de aranhas na vegetação

Aranhas de várias famílias e guildas podem ocupar a vegetação. Entretanto, poucas têm o potencial de manter associações estreitas com plantas. Baseando-se em análises quantitativas de características ecológicas das famílias, Uetz *et al.* (1999) propuseram oito guildas de aranhas: 1) caçadoras por espreita (Salticidae e Oxyopidae), 2) caçadoras por emboscada (Thomisidae e Pisauridae), 3) corredoras na vegetação (Anyphaenidae e Clubionidae), 4) corredoras no solo (Lycosidae e Gnaphosidae), 5) construtoras de teia em forma de lençol (Agelenidae e Amaurobiidae), 6) construtoras de teias em forma de lençol composto por uma malha irregular de fios (e.g., Linyphiidae), 7) construtoras de teias orbiculares (e.g., Araneidae, Tetragnathidae e Uloboridae) e 8) construtoras de teias espaciais em 3-D (e.g., Theridiidae e Pholcidae).

As aranhas das guildas das caçadoras por espreita, por emboscada e das corredoras na vegetação geralmente são as habitantes mais comuns de vegetação (e.g., Nentwig 1993). Enquanto aranhas da família Thomisidae habitam mais freqüentemente flores, aranhas das demais famílias (e.g., Salticidae, Anyphaenidae, Oxyopidae, Pisauridae e Clubionidae) estão geralmente associadas a folhagens (revisão em Romero & Vasconcellos-Neto 2005 a, b, Romero 2005). Uma vez que estas aranhas não constroem teias, mas vivem diretamente e em constante contato com a vegetação, usam a superfície das plantas para forrageamento, abrigo e reprodução. Por isso, podem ter relações mais fortes com este tipo de substrato do que as aranhas construtoras de teias e são, portanto, potencialmente mais propensas a manterem associações benéficas com plantas. De fato, as aranhas que compõem estas guildas são geralmente os principais predadores nas interações multitróficas (revisão em Romero & Vasconcellos-Neto 2005a) e provavelmente os principais agentes de controle biológico (revisão em Romero 2005).

Associações específicas entre aranhas e plantas

Em contraste com muitos insetos herbívoros, que mantém relações altamente específicas com uma ou poucas plantas hospedeiras (Schoonhoven *et al.* 1998), aranhas geralmente não mantém forte associação com determinadas espécies de plantas. No entanto, estudos recentes têm demonstrado que várias espécies de aranhas das famílias Oxyopidae, Thomisidae e 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., rosetas ou plantas com tricomas glandulares). Várias espécies de aranhas do gênero *Peucetia* (Oxyopidae) se associam a mais de 40 espécies (13 famílias) de plantas com tricomas glandulares em diversas localidades no Brasil, Colômbia, Panamá, EUA, Espanha e em alguns países do continente africano (J. Vasconcellos-Neto *et al*., dados não publicados). A aranha *Misumenops argenteus* (Thomisidae) também foi recentemente estudada sobre plantas com tricomas glandulares no sudeste do Brasil (Romero & Vasconcellos-Neto 2003, 2004 a, b). Esta aranha ocorreu preferencialmente sobre duas plantas com tais tricomas (*Trichogoniopsis adenantha*, Asteraceae e *Hyptis suaveolens*, Lamiaceae). Os tricomas glandulares das plantas preferidas aprisionam pequenos insetos e dificultam a locomoção de insetos maiores, que são utilizados como presas.

A aranha *Alpaida quadrilorata* (Araneidae) aparentemente habita somente *Paepalanthus bromelioides* (Eriocaulaceae), uma planta com folhas em forma de roseta, semelhante a bromélias, na Serra do Cipó, MG. Nesta planta, as aranhas encontram abrigo e substrato para construir suas teias (Figueira & Vasconcellos-Neto 1991), que são armadas logo acima do tanque no centro da planta. Quando são perturbadas, descem por um fio e mergulham no líquido do fitotelmata, possivelmente para protegerem-se de predadores.

Estudos recentes mostraram que nove espécies de aranhas da família Salticidae vivem associadas a bromélias (Rossa-Feres *et al*. 2000, Romero & Vasconcellos-Neto 2004 c, 2005 c, d, e, G.Q. Romero *et al.*, dados não publicados) em vários tipos de vegetação, como cerrados, florestas semidecíduas, vegetação de dunas costeiras, restingas, afloramentos rochosos (inselbergs), chacos, florestas sazonais e florestas ombrófilas densas e alta montana, em diversas regiões do Brasil, Bolívia, Argentina e Paraguai (G.Q. Romero, dados não publicados). Algumas destas espécies são tipicamente especialistas e habitam quase exclusivamente uma única espécie de bromélia (e.g., *Psecas chapoda* em *Bromelia balansae*) em uma grande extensão geográfica. Entretanto, outras são generalistas e podem ocupar até 7-8 espécies de bromélias. As espécies especialistas ocorrem em regiões fitogeográficas (e.g., cerrados e florestas semidecíduas) com grande dominância de uma única espécie de bromélia (*B. balansae*), enquanto as generalistas habitam regiões (e.g., floresta ombrófila) com alta riqueza e diversidade de espécies de bromélias-tanque (G.Q. Romero, dados não publicados). Como estas plantas partilham características morfológicas em comum, i.e., folhas largas e presença de tanque, podem ser igualmente atraídas pelas aranhas (G.Q. Romero, dados não publicados). Estas aranhas usam bromélias como sítios de forrageamento, bem como sítios de acasalamento, berçários e abrigos possivelmente contra predação e extremidades climáticas (Rossa-Feres *et al.* 2000, Romero & Vasconcellos-Neto 2004 c, 2005 c, d, e).

A especialização de aranhas Salticidae por Bromeliaceae ocorreu várias vezes independentemente, visto que vários gêneros não relacionados (e.g., *Psecas*, *Eustiromastix*, *Uspachus*, *Asaphobelis* e *Coryphasia*) são bromelícolas. Entretanto, alguns gêneros (*Psecas* e *Coryphasia*) têm mais do que uma espécie bromelícola. Estas espécies relacionadas de cada gênero podem ter se especiado e então ocupado as bromélias de diferentes regiões geográficas. Alternativamente, um ancestral bromelícola de cada gênero pode ter irradiado e especiado entre as bromélias através de diferentes regiões geográficas (G.Q. Romero, dados não publicados).

Informações sobre quais características das plantas são responsáveis pela atração de determinados grupos de aranhas são importantes para investigações de como variações arquiteturais afetam a distribuição das aranhas, estrutura e dinâmica de cadeias tróficas terrestres e para desenvolvimento de metodologias para determinação de inventários da fauna de aranhas e para a conservação da diversidade de aranhas. Além disso, para que haja interações mutualísticas entre aranhas e plantas, é preciso que aranhas estejam freqüentemente e constantemente associadas às suas plantas hospedeiras.

Como aranhas selecionam suas plantas hospedeiras?

Para que haja associações específicas entre aranhas e plantas, é necessário que as aranhas tenham adaptações que facilitem seu encontro com suas plantas hospedeiras. Em geral, as aranhas podem encontrar as plantas de sua preferência através de estímulos visuais, táteis e olfativos (revisão em Romero & Vasconcellos-Neto 2005b). Greco & Kevan (1994) introduziram flores artificiais de diversas cores em arenas experimentais e verificaram que *Misumena vatia* escolheu flores amarelas. Além da coloração, aranhas usam também características morfológicas das plantas. Em um experimento de campo, Morse (1990) verificou que a aranha *M. vatia* escolhe a planta *Asclepias*, dentre várias outras disponíveis, para oviposição. Segundo este autor, a escolha pela planta deve ser governada pelas características da folha. Provavelmente as aranhas preferem folhas de *Asclepias* por apresentarem grande densidade de tricomas, por serem mais flexíveis e de maior tamanho. Evans (1997) também verificou que um tomisídeo social do gênero *Diaea* escolhe os abrigos pelas características morfológicas das folhas de *Eucalyptus*. Mas em contraste com *M. vatia*, que selecionam folhas grandes, *Diaea* prefere folhas menores, pois não consegue manipular folhas grandes devido ao seu tamanho reduzido.

Em contraste a estes trabalhos que demonstraram que tomisídeos escolhem o substrato por estímulos táteis e visuais, um estudo desenvolvido por Krell & Krämer (1998) indica que *Thomisus daradioides* e *T. blandus* (Thomisidae) são atraídos por voláteis de eugenol [2-Methoxy-4-(2-propenyl)phenol], um componente da fragrância floral encontrado em flores de plantas de diferentes famílias em todo o mundo. Em um estudo feito na Austrália, Heiling *et al*. (2004) demonstraram em arenas experimentais que o tomisídeo *Thomisus spectabilis*, bem como o visitante floral *Apis mellifera* (Hymenoptera), preferiram flores de *Chrysanthemum frutescens* com odores naturais a flores cujos odores foram removidos. Os autores verificaram que características visuais das flores (tamanho e refletância) não influenciaram a escolha das flores pelas aranhas e abelhas. É possível que as aranhas memorizem compostos químicos comuns em flores, como o eugenol, e usem tais fragrâncias como pistas para encontrar os sítios de forrageamento, que provavelmente serão mais visitados pelos polinizadores.

Arquitetura das plantas e distribuição das aranhas

Apesar de muitas espécies de aranhas estarem fortemente associadas a plantas, muitas vezes componentes estruturais da vegetação afetam profundamente sua densidade e diversidade (Robinson 1981, Rypstra 1983, Gunnarsson 1990, 1992, Gunnarsson 1996). Em um estudo meta-analítico recente, incluindo vários taxons de artrópodes predadores, Langellotto & Denno (2004) demonstraram que aranhas foram os artrópodes mais afetados por mudanças arquiteturais da vegetação. Em geral, aranhas não comem plantas, mas muitas vezes as plantas são importantes como sítios para construção de teias (Rypstra 1983, Greenstone 1984, Figueira & Vasconcellos-Neto 1991, Herberstein 1997), para abrigo contra dessecação (Riechert & Tracy 1975) ou inimigos naturais (Gunnarsson 1990, 1996), para forrageamento (Morse & Fritz 1982, Morse 1990, Schmalhofer 2001, Romero & Vasconcellos-Neto 2003, 2004 a, b), e para reprodução e oviposição (Rossa-Feres *et al*.

2000, Smith 2000, Romero & Vasconcellos-Neto 2003, Romero & Vasconcellos-Neto 2005 d, e).

Recentemente, Romero & Vasconcellos-Neto (2005 d) verificaram que *Psecas chapoda* ocorre mais freqüentemente sobre bromélias de áreas abertas (campos) do que sobre bromélias de floresta, em locais adjacentes. Este padrão sugere que as folhas secas que caem das árvores sobre as bromélias na área de floresta bloqueiam a base das rosetas, que é utilizada como abrigo pela aranha. Para testar esta hipótese, Romero & Vasconcellos-Neto (2005 c) introduziram folhas secas nas bromélias da área aberta e verificaram que estas foram menos colonizadas pelas aranhas do que plantas que não receberam folhas secas. Entretanto, bromélias da floresta cujas folhas secas no seu interior foram removidas não foram ocupadas pelas aranhas. Uma vez que a abundância de insetos foi muito maior na área aberta do que na floresta, os autores sugeriram que folhas secas e disponibilidade de presas devem estar atuando conjuntamente na distribuição espacial de *P. chapoda*. Aranhas desta espécie chegam a ocupar até 90% das bromélias sem inflorescência, mas raramente ocorrem sobre plantas com tais estruturas florais (Romero & Vasconcellos-Neto 2005 c, d, e). As bromélias com inflorescência têm sua arquitetura modificada devido ao tombamento das suas folhas em direção ao solo, e que provavelmente é uma adaptação para expor a inflorescência (central) aos visitantes florais. Romero & Vasconcellos-Neto (2005 c) corroboraram experimentalmente esta hipótese pela simulação de inflorescências (tombamento das folhas) nas bromélias ainda em fase vegetativa, e sugeriram que esta mudança na arquitetura da planta modifica os sítios de abrigo e de nidificação, além de deixar os salticídeos mais desprotegidos à predação e condições climáticas severas. Estes resultados sugerem que a aranha *P. chapoda* pode avaliar, em detalhes finos, o estado físico do seu microhabitat; esta associação aranha-planta é rapidamente desestabilizada por mudanças no microhabitat.

Aranhas que comem plantas

Apesar das aranhas serem predadores por excelência, em algumas situações podem utilizar fontes alternativas de alimento, como néctar e pólen (revisão em Romero & Vasconcellos-Neto 2005 b). Por exemplo, machos de *Misumenoides formosipes* (Thomisidae) se alimentam de néctar dos nectários extra-florais (NEFs) de algumas espécies de planta (e.g. *Daucus carota*, *Solidago* spp. e *Cichorium intybus*). Quando pequenas quantidades de água e solução de sacarose a 30% foram oferecidas para machos desta espécie de aranha em arenas experimentais, Pollard *et al*. (1995) notaram que houve preferência pela sacarose. Além disso, mesmo após saciados com água, puderam ainda ingerir a solução de sacarose. Os machos que ingeriram somente água viveram por menos tempo que os que se alimentaram com néctar. Os autores sugerem que néctar pode ser usado como fonte de energia e que o hábito de se alimentar de néctar dos NEFs pode ser um comportamento adaptativo para esta espécie de aranha.

As aranhas errantes *Hibana velox*, *H. similaris* (Anyphaenidae), *Cheiracanthium mildei* (Miturgidae) e *Trachelas similis* (Corinnidae) se alimentam tanto em nectários florais como em nectários extra-florais de várias espécies de plantas em várias localidades da Costa Rica e Flórida (Taylor & Foster 1996). Para testar o papel do néctar na longevidade de aranhas recém emergidas de *H. velox*, Taylor & Foster (1996) desenvolveram um experimento com os jovens em dois grupos: tratados somente com água e com solução de sacarose a 25%, e demonstraram que a longevidade dos tratados com sacarose foi duas vezes maior.

Na natureza, Jackson *et al*. (2001) observaram 31 espécies de Salticidae se alimentando de néctar floral. Em laboratório, os autores testaram em arenas experimentais a preferência de 90 espécies de Salticidae por água destilada vs. solução de sacarose a 30%, e demonstraram que todas escolheram e permaneceram por mais tempo sobre a solução de sacarose, indicando que a nectarivoria deve ser um habito comum na família Salticidae. Os autores sugerem que o hábito de se alimentar de néctar pode ser vantajoso para as aranhas porque, além deste fluido ser rico em ácidos aminados, lipídios, vitaminas e minerais, se alimentar em uma flor não traz prejuízos para as aranhas, como injúrias decorrentes de lutas com presas.

Um dos primeiros trabalhos extensivos sobre aranhas que se alimentam de pólen foi desenvolvido por Smith & Mommsen (1984). Estes autores verificaram em terrários que indivíduos recém emergidos de *Araneus diadematus* (Araneidae) dobraram sua expectativa de vida e produziram mais fios de seda quando se alimentaram de pólen em relação à outros que se alimentaram de afídeos e esporos de fungo. Os autores discutem que este hábito alimentar deve ser adaptativo em regiões temperadas porque nos períodos que os jovens emergem (primavera) há muito pouco ou nenhum inseto disponível, mas há grande quantidade de pólen produzido pelas árvores polinizadas pelo vento. Vogelei & Greissl (1989) também testaram a sobrevivência de aranhas recém emergidas de *Thomisus onustus* (Thomisidae) quando tratados com quatro tipos de dieta: 1) nada (controle), 2) pólen de *Erigeron annuus* e de 3) *Bellis perennis* (Asteraceae), 4) simulação de néctar (solução de sacarose a 30%) e 5) moscas *Drosophila melanogaster*. As aranhas do grupo controle sobreviveram em média 21 dias. Os grupos de aranhas que se alimentaram de pólen sobreviveram por 35-49 dias, dependendo da espécie de planta, e os que se alimentaram de néctar artificial sobreviveram por 130 dias. Entretanto, somente os indivíduos alimentados com as moscas mudaram normalmente e sobreviveram até o final do experimento (> 250 dias). Com estes resultados, os autores sugerem que pólen e néctar podem ser uma fonte de energia para as aranhas por períodos mais ou menos extensos, especialmente em períodos de escassez de presas.

Em contraste com estes trabalhos que demonstraram algum benefício para aranhas que se alimentam de pólen, Carrel *et al.* (2000) mostraram que a aranha *Frontinella pyramitela* (Linyphiidae) ganhou peso quando alimentada com *D. melanogaster,* mas perdeu peso quando alimentada com pólen de *Pinus elliottii*. Os autores sugerem que a polinivoria pode ser restrita a determinados grupos de aranhas e a determinadas condições ambientais de escassez de alimento.

Alguns recursos alimentares alternativos fornecidos pelas plantas, como néctar dos NEFs, devem ter primariamente evoluído em associação com formigas. Entretanto, aranhas que usam este tipo de recurso podem beneficiar plantas. Por exemplo, a presença das aranhas *Eris* sp. e *Metaphidippus* sp. (Salticidae) aumentam a produção de frutos e de sementes de *Chamaecrista nictitans* (Caesalpineaceae) (Ruhren & Handel 1999). Estas aranhas são atraídas pela fonte alternativa de alimento e adicionalmente removem os herbívoros das plantas.

Mutualismos e parasitismos em sistemas aranha-planta

Os exemplos mais bem estudados de mutualismos entre plantas superiores e animais vêm de interações envolvendo polinização (Faegry & van der Pijl 1979), dispersão de sementes (Jordano 2000, Passos & Oliveira 2002) ou mutualismos defensivos entre formigas e plantas (revisão em Oliveira & Freitas 2004, Heil & McKey 2003) e entre ácaros e plantas (revisão em Romero & Benson 2005). As plantas geralmente oferecem algum tipo de recompensa alimentar, tal como néctar e pólen, para os animais que, em retorno, transferem gametas, dispersam sementes para áreas favoráveis e defendem plantas contra seus inimigos. Em adição, plantas produzem traços morfológicos inequívocos que servem de abrigo para formigas (e.g., mirmecodomáceas) e ácaros (e.g., domáceas de folhas) que encorajam associações mais constantes, atraem e ajudam a manter organismos do terceiro nível trófico. Em retorno, estes animais removem herbívoros e patógenos (Heil & McKey 2003, Romero & Benson 2005) e contribuem para a nutrição das plantas (Huxley 1980, Treseder *et al*. 1995, Fischer *et al*. 2003).

Embora aranhas estejam freqüentemente envolvidas em cadeias tróficas complexas ou em interações diretas ou indiretas com outros artrópodes e plantas (revisão em Romero & Vasconcellos-Neto 2005a), muito poucos estudos evidenciaram mutualismos entre aranhas e plantas (veja, por exemplo, Louda 1982, Ruhren & Handel 1999, Whitney 2004). Mutualismos aranhas-plantas podem ser basicamente de dois tipos: defensivo ou de proteção, em que aranhas, através da remoção de fitófagos, aumentam a aptidão das plantas, e nutricional (ou digestivo), em que aranhas contribuem para a nutrição das suas plantas hospedeiras. Como um exemplo de mutualismo de proteção, as aranhas Thomisidae que habitam plantas *T. adenantha* com tricomas glandulares podem se beneficiar pela presença destas estruturas; estes tricomas fixam insetos que tornam-se presas em potencial das aranhas (veja acima). Em retorno, as aranhas combatem parte da fauna de fitófagos florais da planta e aumentam indiretamente o desempenho (i.e., número de sementes viáveis) das plantas (Romero & Vasconcellos-Neto 2004a). Alguns estudos adicionais também reportaram mutualismos entre aranhas e plantas (veja Louda 1982, Ruhren &

Handel 1999, Whitney 2004). Entretanto, quando as aranhas ocorrem sobre flores, capturam tanto insetos fitófagos florais como também visitantes florais, podendo modificar o balanço de interações positivas e negativas entre plantas e os componentes do segundo nível trófico (herbívoros) e os mutualistas da planta (polinizadores) (revisão em Romero & Vasconcellos-Neto 2005 a). Efeitos prejudiciais de aranhas para plantas tipicamente ocorrem quando aranhas interferem nos mutualismos entre plantas e outros artrópodes. Por exemplo, estudos recentes têm demonstrado que aranhas sobre flores podem reduzir as visitas dos polinizadores (Dukas 2001, Dukas & Morse 2003, Suttle 2003) e indiretamente interferir no mutualismo polinizador-planta e na reprodução das plantas (i.e., transferência de pólen). Em adição, aranhas que habitam plantas mirmecófilas podem predar ou afugentar formigas e interferir nas relações mutualísticas entre estes insetos e plantas (veja Gastreich 1999).

Mutualismos envolvendo provisionamento de plantas com nutrientes (i.e., mutualismo digestivo ou mutualismo nutricional) foram documentado em sistemas formigas-plantas, porém, pouco se conhece sobre este tipo de benefício em sistemas aranhas-plantas. O primeiro estudo nesta direção foi realizado recentemente por Romero *et al*. (dados não publicados, veja capítulos 7 e 8 desta tese). Os autores verificaram por meio de técnicas isotópicas (isótopo estável ^{15}N) que a aranha *P. chapoda*, uma habitante comum da bromélia *B. balansae* em várias regiões da América do Sul, nutre esta planta com suas fezes e carcaças de presas. As aranhas contribuem com até 40% do nitrogênio total das plantas. Além do mais, este estudo mostrou por meio de experimentos em campo que *B. balansae* com as aranhas cresceram 15% mais do que aquelas em que as aranhas foram excluídas. Uma vez que muitos grupos de animais (e.g., insetos, crustáceos, aranhas, anfíbios, lagartos) vivem associados a Bromeliaceae, mutualismos entre animais e plantas desta família podem ser comuns. Em um estudo subseqüente, Romero *et al.* (dados não publicados) testaram se a intensidade deste mutualismo nutricional aranha-planta varia espacialmente com as variações na densidade de aranhas. Os autores encontraram uma correlação positiva entre densidade de aranhas entre fragmentos florestais e valores de δ^{15}N nas folhas das bromélias. Bromélias de campos abertos estavam associadas com aranhas e apresentaram valores altos de δ^{15}N se comparados com bromélias crescendo no interior da floresta, que não mantém associação com as aranhas (veja Romero & Vasconcellos-Neto 2005c). Apesar disso, bromélias da floresta apresentaram valores mais altos de concentração total de N do que bromélias dos campos abertos. Estes resultados sugerem que a nutrição das bromélias é baseada mais em folhiço dentro da floresta e mais em detritos provenientes das aranhas nos campos abertos.

Aranhas podem também parasitar mutualismos nutricionais. O heteróptero predador *Pameridea roridulae* (Miridae) vive exclusivamente associado à planta carnívora *Roridula gorgonias* (Roridulaceae) na África do Sul e pode contribuir com até 70% do N total das plantas (Ellis & Midgley 1996). Entretanto, em algumas regiões *R. gorgonias* também é habitada por uma aranha (*Synaema marlothi*, Thomisidae) que freqüentemente decresce a densidade do mutualista *P. roridulae* na planta. Anderson & Midgley (2002) demonstraram que na presença das aranhas e na baixa densidade dos heterópteros, as plantas foram menos enriquecidas com nitrogênio (isótopo ^{15}N), provavelmente porque as aranhas não defecam diretamente na planta.

Benefícios recíprocos entre aranhas e plantas estão sendo evidenciados recentemente. Entretanto, por que há tão poucos casos descritos de mutualismos entre aranhas e plantas, se comparado com mutualismos envolvendo outros tipos de artrópodes (e.g., formigas, ácaros)? Para haver mutualismos aranhas-plantas, aranhas devem manter associações específicas com uma ou poucas espécies de plantas, pelo menos em algum período do seu ciclo biológico. No entanto, é possível que a maior parte das espécies de aranhas associadas à vegetação não mantenha associações específicas com plantas. Além disso, a evolução e persistência dos mutualismos par-a-par entre animais e plantas são dependentes do produto final da interação: a relação deve ser previsivelmente positiva para ambos parceiros através do espaço e tempo (Bronstein 1994, Thompson 1988). No entanto, aranhas são generalistas e capturam grande variedade de ítens alimentares. Por incluírem na sua dieta outros organismos do terceiro nível trófico (i.e., predação intra-guilda) e também outros mutualistas das plantas (e.g., polinizadores) (Romero & Vasconcellos-Neto 2005a), além dos herbívoros, os benefícios das aranhas às plantas podem ser habitualmente excedidos pelos custos (Whitney 2004).

Alternativamente, muitos sistemas mutualísticos aranha-planta podem existir, mas são pobremente conhecidos possivelmente por serem inconspícuos. Mutualismos formigas-plantas e ácaros-plantas são mediadas por estruturas especializadas únicas (domáceas) (Heil & McKey 2003, Romero & Benson 2005). Entretanto, nada similar ocorre em aranhas, porém muitos traços morfológicos das plantas, tais como estruturas foliares, pubescência ou arquitetura dos ramos podem facilitar a especialização de aranhas e de outros organismos do terceiro nível trófico (Marquis & Whelan 1996). Por exemplo, tricomas glandulares parecem facilitar a captura de insetos pelas aranhas, e plantas com arquitetura em roseta (e.g., bromélias) protegem aranhas contra predadores, dessecação, além de oferecerem sítios de reprodução e de forrageamento. No entanto, outras estruturas de plantas podem mediar associações aranha-planta, mas que ainda aguardam para serem descobertas. Além disso, é possível que uma grande fração das relações aranha-planta sejam mutualísticas, mas com produtos variando através do espaço e tempo, tornando difícil a detecção dos efeitos benéficos (Whitney 2004, Romero *et al.*, em preparação). Por exemplo, o mutualismo nutricional entre *Psecas* e *Bromelia* varia espacialmente com a densidade de aranhas, com plantas recebendo nenhum benefício derivado de aranhas em regiões onde aranhas estão ausentes. De qualquer forma, aparentemente a grande maioria das associações mutualísticas entre aranhas e plantas devem ser facultativas. Uma possível exceção é *Psecas chapoda*-*Bromelia balansae*, uma vez que estas aranhas habitam quase exclusivamente *B. balansae* e ainda não foram observadas se alimentando, se refugiando nem se reproduzindo fora da planta hospedeira (G.Q. Romero, dados não publicados).

Comparando mutualismos aranha-planta, formiga-planta e ácaro-planta

Apesar das aranhas, juntamente com as formigas e os ácaros, estarem entre os artrópodes mais abundantes sobre folhas e potencialmente beneficiarem suas plantas hospedeiras, por que plantas não produziram abrigos "aracnodomáceas" para aranhas, como fizeram as plantas mirmecófitas e as que abrigam ácaros nas domáceas de folhas? Enquanto aranhas são geralmente predadoras errantes e forrageiam solitariamente, formigas se organizam socialmente, vivem em colônias fixas e capturam presas mais eficientemente por recrutarem operárias. Uma vez que as formigas têm parentesco bastante próximo entre os membros da colônia e por estes indivíduos serem interdependentes (e.g., organização social), têm muito a ganhar caso um intruso (e.g., herbívoro) seja afastado de seu ninho na planta (defesa organizada). Além disso, constroem seus ninhos em locais fixos (e.g., domáceas), um comportamento ancestral de nidificação em buracos no solo ou em ocos em troncos mortos, e não podem se deslocar por longas distâncias, como fazem as aranhas. Conseqüentemente, as formigas evoluíram no sentido de proteger indiretamente suas plantas hospedeiras contra herbívoros e algumas vezes também contribuem indiretamente para a nutrição das plantas com restos de presas e fezes (Treseder *et al.* 1995, Fischer *et al.* 2003). Portanto, podem manter associações estáveis e duradouras com suas hospedeiras, permitindo a evolução de estruturas morfológicas (e.g., mirmecodomáceas e corpúsculos alimentares) que estabilizam ainda mais sistemas formiga-planta, além de favorecer uma especialização de formigas por uma ou poucas plantas mirmecófilas. Vários mutualismos formiga-planta são obrigatórios. Já em aranhas, são raros os casos de socialidade, mas quando há, geralmente as colônias são formadas por seda e aparentemente são ancoradas em plantas com qualquer tipo de arquitetura. Neste caso, as aranhas geralmente não mantêm contato direto com a superfície foliar.

Ácaros benéficos geralmente não mantém associações específicas nem obrigatórias com plantas. Entretanto, eles são extremamente pequenos e apresentam abundâncias muito elevadas, bem maiores do que aranhas sobre a superfície foliar, com números variando de um a dezenas de indivíduos por folha ou folíolo (e.g., Romero & Benson 2004). Protegem as plantas contra fitófagos e patógenos foliares, mas são freqüentemente vulneráveis ao ataque de artrópodes maiores. Domáceas de folhas surgiram possivelmente como refúgios para ácaros benéficos contra predação por outros artrópodes maiores (revisão em Romero & Benson 2005), possivelmente através de uma co-evolução difusa entre ácaros e plantas.

Em adição, sistemas mutualísticos aranhas-plantas parecem menos estáveis se comparados com sistemas formigas-plantas e ácaros-plantas. Uma vez que aranhas são fortemente dependentes das estruturas físicas do habitat, uma simples mudança na arquitetura da planta pode desestabilizar um sistema aranha-planta (Romero & Vasconcellos-Neto 2005 c), rompendo a continuidade da interação mutualística. Por exemplo, o sistema aranha-planta *Psecas*-*Bromelia* (veja acima) se colapsa no início do período reprodutivo da planta. As mudanças arquiteturais da roseta impedem com que as aranhas obtenham abrigo e sítios de reprodução e forrageamento (Romero & Vasconcellos-Neto 2005 c).

Conclusões

Aranhas são importantes componentes das comunidades de artrópodes terrestres. Por serem predadores abundantes, afetam a estrutura de populações de insetos fitófagos e geralmente decrescem as taxas de herbivoria das suas plantas hospedeiras. As aranhas das famílias Salticidae, Thomisidae, Oxyopidae, Anyphaenidae, Pisauridae e Clubionidae são as que geralmente mantém associações mais fortes com plantas. Usam informações visuais, táteis e olfativas para encontrar suas plantas hospedeiras. Evidências recentes indicam que existem basicamente dois tipos mutualismos entre aranhas e plantas: mutualismo de proteção (i.e., aranhas que removem herbívoros) e mutualismo digestivo (i.e., aranhas que contribuem para a nutrição das suas plantas hospedeiras).

Objetivos gerais

Esta tese teve os objetivos de:

1. Determinar se as associações entre aranhas da família Salticidae e Bromeliaceae são específicas,

2. Descrever a história natural e os padrões de distribuição microespacial, espacial e geográfico das aranhas Salticidae sobre Bromeliaceae,

3. Determinar se as associações Salticidae-Bromeliaceae são mutualísticas e se estes mutualismos são condicionais.

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2. ASSOCIAÇÕES ESPECÍFICAS, DISTRIBUIÇÃO ESPACIAL E HISTÓRIA NATURAL

Eustiromastix nativo, *Psecas* sp., *Coryphasia* sp. 1 e *Coryphasia* sp. 2 sobre Bromeliaceae. (A) *E. nativo* sobre *Aechmea blanchetiana* em restinga, Trancoso, BA, (B) Casal de *Psecas* sp. coletado em mussununga, Linhares, ES, (C) *Coryphasia* sp. 1 sobre *Aechmea distichantha* em inselberg, Monte Verde, MG, (D) moitas de *A. distichantha* em inselberg, Monte Verde, MG. (E) *Coryphasia* sp. 2 sobre *Quesnelia arvensis* em restinga, Ilha do Cardoso, SP, (D) indivíduos de *Q. arvensis* na restinga da Ilha do Cardoso, SP.

Artigo 1

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

Running title: spiders associated with bromeliads

Spatial distribution patterns of jumping spiders associated with terrestrial bromeliads[1]

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ABSTRACT

The jumping spiders *Eustiromastix nativo*, *Psecas sumptuosus* and *Uspachus* sp. n. (Salticidae) live on terrestrial bromeliads in areas with different phytophysiognomies in southeastern and northeastern Brazil. To understand these spider-plant interactions, we investigated whether 1) these spiders were associated specifically with bromeliads, 2) the spiders utilize particular bromeliad species and 3) plant size and density of bromeliads affected spider distribution. The jumping spiders were not found outside bromeliads, indicating a strict spider-plant association. *Eustiromastix* and *Uspachus* occupied bromeliads in open areas whereas *Psecas* were found on forest bromeliads. *Eustiromastix* occurred at a higher frequency on larger bromeliads, and in patches with higher bromeliad density. This is one of the few studies to demonstrate specific relationships between jumping spiders and a particular plant type.

Key words: *Bromeliaceae*; Eustiromastix; Psecas; *Salticidae*; *spider*; *animal-plant interaction*; *plant structure*; *Brazil*; *tropical rain forest.*

Animals that occupy favorable habitats not only enhance their own chances of survival, but could increase their contribution of offspring to the next generation. Hence, habitat choice can be rigorously molded by natural selection (Pianka 1994). Spiders are known to be selective of microhabitat and foraging sites, increasing their survivorship and reproductive success (Morse & Fritz 1982, Fritz & Morse 1985, Riechert & Gillespie 1986, Morse 1988, Morse 1990, Chien & Morse 1998, Romero & Vasconcellos-Neto 2004a). The spatial distribution of spiders that live in vegetation is frequently influenced by plant architecture and habitat (Colebourne 1974, Greenquist & Rovner 1976, Robinson 1981, Rypstra 1983, Gunnarsson 1990, 1992), especially since plants provide shade, shelter and protection against the elements, and also serve as attractive sites for prey (reviewed in Wise 1993). However, in contrast to host-specific herbivorous insects (Schoonhoven *et al.* 1998), spiders generally do not have a strong association with the plants on which they occur. On the other hand, recent studies have reported some spider taxa inhabiting and breeding on specific plant species (Figueira & Vasconcellos-Neto 1993, Taylor & Jackson 1999, Rossa-Feres *et al.* 2000, Romero & Vasconcellos-Neto 2003, 2004a,b, in press, a, b).

Jumping spiders (Salticidae) are generally errant hunters and several species live in complex environments, including leaf litter, branches and dense foliage (Jackson & Pollard 1996). Plants of the family Bromeliaceae have a complex three-dimensional architecture and can constitute a good microhabitat for jumping spiders (Romero & Vasconcellos-Neto, in press, a, b, c, G. Q. Romero, unpubl. data). For example, *Psecas chapoda* (Peckham & Peckham) (Salticidae) occurs on *Bromelia balansae* Mez. (Bromeliaceae) in various regions of Brazil and at some localities in Paraguay and Bolivia (Romero & Vasconcellos-Neto, in press, a, b, c, G.Q. Romero, unpubl. data). The courtship, mating, and population recruitment of *P. chapoda* occur on this plant (Rossa-Feres *et al.* 2000). Although there are some studies on jumping spiders living on plants (e.g. Richman & Whitcomb 1980, Jackson 1986, Cutler 1992, Taylor 1998, Taylor & Jackson 1999, Rossa-Feres *et al*. 2000, Romero & Vasconcellos-Neto, in press, a, b, c), the associations of salticids with particular kinds of plants are poorly known.

The jumping spiders *Eustiromastix nativo* Santos & Romero, *Psecas sumptuosus* (Perty) and *Uspachus* sp. n. live on terrestrial bromeliad species in different vegetation types in Brazil. To understand this spider-plant relationship, we asked the following questions: 1) Are *Eustiromastix*, *Psecas* and *Uspachus* associated specifically with bromeliads? 2) Do spiders utilize particular bromeliad species? 3) Do plant size and bromeliad density affect the spatial distribution of these spiders?

METHODS

STUDY SITE. – This work was done in the following locations: August 1999 and 2002 in nativo and mussununga vegetation in the Reserva Florestal da Companhia Vale do Rio Doce in Linhares (19º06' S, 39º45' W), Espírito Santo state, southeastern Brazil; October 2001 in a restinga area, near Trancoso (16º26' S, 39º03' W), Bahia state; and September 2002 in a dune vegetation in the Parque Estadual das Dunas in Natal (05º45' S, 35º12' W), Rio Grande do Norte state, both in northeastern Brazil.

Nativo vegetation, a sandy soil community is dominated by cacti, bromeliads, herbs and small shrubs. Mussununga vegetation consists of small trees, with a dense undergrowth (Peixoto & Gentry 1990). In the restinga of Trancoso, the phytophysiognomy is similar to that of nativo vegetation (Lacerda *et. al*. 1984) and both of these are habitats with high light incidence. The higher regions of the dunes from Natal have vegetation similar to that of restinga and nativo vegetation, but in low areas, the vegetation is tall (~10-15 m) and dense (G. Q. Romero, pers. obs.). In the nativo, mussununga and restinga areas, there are bromeliad species with different sizes architectural characteristics. *Vriesea neoglutinosa* Mez. occurs in nativo and in the restinga at Trancoso, and has a spineless leaf margin. *Aechmea macrochlamys* L.B. Sm. is a medium sized plant that occurs only in the mussununga, while *Aechmea blanchetiana* (Baker) L.B. Sm. is a large sized plant present in the mussununga and in the restinga of Trancoso. The latter two species have small, closely arranged spines that form a serrated leaf margin. *Bromelia balansae* Mez. occurs in areas of undergrowth in the mussununga. At Trancoso, *B.* aff. *balansae* is found in an ecotonal region between the restinga and the Atlantic forest. This plant is large, with big, curved spines spaced 2.5-3.5 cm apart. Of all these bromeliad species, *B. balansae* is the only one that does not accumulate rain water (see Rossa-Feres *et al.* 2000). In higher regions of the dunes at Natal, we found only one bromeliad species, *Hohenbergia ramageana* Mez., that in vegetative phase is very similar to *A. blanchetiana*.

MICROHABITAT USE. – To determine whether *Psecas*, *Eustiromastix* and *Uspachus* were restricted to bromeliads or whether they also occurred on other plants, we used random 80 m x 5 m transects to inspect 303 herbaceous plants and shrubs (non-bromeliads) in nativo (2 transects), 418 plants in mussununga (3 transects), 250 plants in the restinga at Trancoso (2 transects) and 250 plants in dune vegetation at Natal (1 transect). We inspected whole small plants when up to 1.7 m height, and branches and trunk up to 1.7 m height in taller plants. We investigated the differential utilization of particular bromeliad species by *Psecas* and *Eustiromastix*. For this, we recorded the presence/absence of the spiders within several terrestrial bromeliads available in the same transects used for inspecting the non-bromeliad plants. In the habitat of *Uspachus* (dune vegetation at Natal) we found only one bromeliad species.

BROMELIAD SIZE AND DENSITY AND SPIDER DISTRIBUTION. – The size (surface area) of bromeliads might affect spider distribution. We examined this hypothesis for only *V. neoglutinosa* and *A. blanchetiana* because they were the most abundant in nativo and in the restinga at Trancoso, respectively. We sampled rosettes of *V. neoglutinosa* found occupied by *Eustiromastix* (N = 130) and unoccupied by this species (N = 82) along a random 200 m x 5 m transect in nativo. The same was done at Trancoso, for 129 rosettes of *A. blanchetiana* (62 occupied and 67 unoccupied by *Eustiromastix* sp.). The size of each plant was estimated as the product of the length x breadth of a leaf from the middle layer of the rosette. The leaf area was then multiplied by the total number of green leaves on each plant to obtain an approximation of the total plant surface area (Romero & Vasconcellos-Neto, in press, a). *Psecas* was not considered in the analyses because it occurred at a relatively low density at Linhares and was not found at Trancoso. The distributions of the relative frequencies of the *V. neoglutinosa* and *A. blanchetiana* size classes available and those occupied by *Eustiromastix* were compared by the *G*-test of independence (Sokal & Rohlf 1995).

Vriesea neoglutinosa usually constitutes thickets of different sizes, varying from two to 19 individuals in nativo. To investigate whether *Eustiromastix* occupied larger bromeliads in each thicket, we inspected 221 individuals of *V. neoglutinosa* in 26 thickets in nativo. The size (surface area) of each plant in each thicket was estimated as described above. We compared the mean size of bromeliads occupied and unoccupied in each thicket by *Eustiromastix* using the Wilcoxon matched-pairs signed-rank test (Sokal & Rohlf 1995). Patches with higher density of bromeliads might support larger spider populations. We examined this hypothesis in two patches (P1 and P2) in nativo, separated by an area of mussununga, and differing from each other in their cover of *V. neoglutinosa* (see Figure 3a). We estimated the density of *V. neoglutinosa* in two random 100 m x 4 m transects (one per patch), by counting the number of bromeliads in a 10 x 4 m area at 10 m intervals, resulting in 10 replicates adding up to 400 m^2 sampled per patch. We estimated the relative frequency of bromeliads occupied by *Eustiromastix*, by randomly inspecting the first 120 individuals of *V. neoglutinosa* found along two random 250 m linear transects, one in P1 and the other in P2. The size of the plants sampled in these two patches did not differ statistically (Student's *t*-test, $P > 0.8$).

RESULTS

MICROHABITAT USE. – We did not find *Eustiromastix*, *Psecas* and *Uspachus* on non-bromeliad plants. There was only one instance of one of these jumping spiders on a leaf that was not a bromeliad. In this case, the plant (unidentified dicotyledon) occupied by one *Eustiromastix* spider had large leaves and was located 20 cm above a thicket of *Vriesea* in nativo (Linhares).

We observed both adults and juveniles of the three salticid species within bromeliads, as well as eggsacs of *Eustiromastix* ($N = 7$) and *Psecas* ($N = 4$) on the concave surface of bromeliad leaves. *Eustiromastix* occupied *V. neoglutinosa* in nativo, and *A. macrochlamys* and *A. blanchetiana* in the mussununga. However, the occupancy of *V.*

neoglutinosa was significantly greater than that of the other bromeliad species ($G = 91.92$, df = 2, $P < 0.0001$, Figure 1a). In contrast, in the restinga at Trancoso, there was no difference in frequency of *V. neoglutinosa* and *A. blanchetiana* plants inhabited by *Eustiromastix* ($G = 0.80$, df = 1, $P = 0.371$, Figure 1b). *Eustiromastix* was never found on *B. balansae* in Linhares and on *B.* aff. *balansae* in Trancoso. *Psecas* occupied fewer *V. neoglutinosa* relative to other bromeliads ($G = 6.27$, df = 1, $P = 0.012$), occurred with similar frequency on *A. macrochlamys* and on *A. blanchetiana* ($G = 2.02$, df = 1, $P = 0.155$) and, like *Eustiromastix*, did not occur on *B. balansae* (Figure 1a). *Uspachus* occupied 22% of the *H. ramageana* (total of plants examined = 144) in the open areas (higher areas) of the dune vegetation at Natal, and a single specimen of this spider was found on *Vriesea neoglutinosa* in nativo, Linhares. In every instance, we never found more than one species per plant.

BROMELIAD SIZE AND DENSITY AND SPIDER DISTRIBUTION. – *Eustiromastix* occurred non-randomly on bromeliads of different sizes, with the highest frequency on larger individuals of *V. neoglutinosa* in nativo ($G = 89.8$, df = 4, $P < 0.0001$, Figure 2a) and *A. blanchetiana* in Trancoso ($G = 12.94$, df = 4, $P = 0.011$, Figure 2b). *Eustiromastix* also occupied larger individuals of *V. neoglutinosa* among thickets (mean ± SE in cm, plants occupied = 3424.34 ± 299.07, plants unoccupied = 1445.95 ± 129.02, Wilcoxon signed-rank test, $W = 349$, $N = 26$, $P < 0.001$). The density of *V. neoglutinosa* was higher in patch P1 compared to patch P2 in nativo (Mann-Whitney test, $H = 155$, $N_1 = N_2 = 10$, $P < 0.001$, Figure 3a), and the bromeliads of the former patch were more frequently occupied by *Eustiromastix* than bromeliads from patch P2 ($G = 9.23$, df = 1, $P = 0.002$, Figure 3b).

DISCUSSION

Our results suggest that the biology of *Eustiromastix nativo*, *Psecas sumptuosus* and *Uspachus* is linked specifically to bromeliads at Linhares, Trancoso and Natal. Santos (1999) studied the community of spiders based on collections in non-bromeliad plants in nativo (N = 970 plants), mussununga (N = 1020 plants) and in the adjacent Tabuleiro Forest (Peixoto & Gentry 1990) (N = 1520 plants) and collected approximately 2000 adult spiders, but found no specimens of *Psecas*, *Uspachus* or *Eustiromastix* on the plants sampled. Bromeliads may be suitable microhabitats for jumping spiders, since their leaves are flat and form an open, but complex three-dimensional architecture (rosette) that permits the spiders to take shelter (Romero & Vasconcellos-Neto, in press, a, b, c) and to hunt (Romero & Vasconcellos-Neto, in press, c). Studies have reported salticids occurring on open and flat surfaces, such as crags, bark, building walls (Foster 1982), palm leaves (Jackson 1986) or even bromeliads (Crane 1949, Rossa-Feres *et al*. 2000, Romero & Vasconcellos-Neto, in press, a, b, c).

Eustiromastix and *Psecas* differed in their pattern of occupation of bromeliads in the two types of vegetation at Linhares (nativo and mussununga). Interspecific competitive exclusion at the habitat or microhabitat (bromeliad) level could have shaped this distribution pattern. Alternatively, each spider species could possibly select distinct microhabitat traits of the plant, such as surface area and plant architecture, or environmental characteristics, such as temperature, humidity and/or light. The observations at Trancoso do not fully support the hypothesis of interspecific competitive exclusion, at least competition from *Psecas* towards *Eustiromastix*, since in the absence of *Psecas*, *Eustiromastix* continued to occur only in open areas, but on different bromeliad species (e.g. *A. blanchetiana*). These results suggest that *Eustiromastix* first selects its habitat and then its microhabitat. Riechert and Gillespie (1986) also reported that web-building spiders first establish in a suitable habitat and subsequently show active selection for suitable microhabitats within a patch.

None of the jumping spiders studied occurred on *B. balansae* in Linhares or on *B.* aff. *balansae* in Trancoso. A possible explanation is that this plant does not accumulate rain water in its rosette (see Rossa-Feres *et al*. 2002). The water accumulated in other bromeliad species (e.g. *Vriesea*, *Aechmea* and *Hohenbergia*) can be both an important source of protection against climatic extremities, and a shelter from predators. Both *Eustiromastix* and *Psecas* were observed submerging in the water of the bromeliad phytotelmata when approached by an observer trying to capture them, and one individual (*Eustiromastix*) remained submerged for more than 6 min (G. Q. Romero, pers. obs.).

Eustiromastix occurred more frequently on larger individuals of *V. neoglutinosa* and *A. blanchetiana* in nativo and in the restinga at Trancoso, respectively. Individuals of *Eustiromastix* also selected the largest plants in each thicket. Larger bromeliads possibly have more availability of shelter and a higher probability of being visited by insects due to their larger surface area (Romero & Vasconcellos-Neto, in press, a, c). Hence, larger plants may represent more shelter and foraging sites of better quality. Figueira and Vasconcellos-Neto (1993) showed that *Latrodectus geometricus* (Theridiidae) occurred preferentially on larger individuals of *Paepalanthus bromelioides* (Eriocaulaceae), a bromeliad-like plant, and adult females that occurred on larger plants captured more prey and had a higher reproductive success.

Not all patches of nativo had the same density of *V. neoglutinosa*. Where these plants occurred in higher density, they were occupied by proportionally more

Eustiromastix. These results suggest that patches poor in foraging sites and shelter can be difficult for spider populations to become established. Moreover, individuals of *Eustiromastix* may have to travel for longer distances in patches poor in bromeliads to reach another bromeliad, thereby exposing themselves to predators and climatic extremities.

In conclusion, *Psecas*, *Eustiromastix* and *Uspachus* were specifically associated with bromeliads. Whereas *Eustiromastix* lives in open areas, *Psecas* occurs in adjacent forests. This pattern of distribution possibly reflects the choice of habitat and/or microhabitat (bromeliad), ratter than interspecific competition (at least from *Psecas* to *Eustiromastix*). Like other spiders, the *Eustiromastix* population was affected by the size and density of the microhabitats.

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Figures legends

Figure 1. Percent bromeliads of different species occupied by *Eustiromastix nativo* (solid bars) and *Psecas sumptuosus* (open bars), (a) in the nativo and mussununga at Linhares and (b) in the restinga at Trancoso. The number of plants inspected is indicated above the bars.

Figure 2. Relative frequency of (a) *Vriesea neoglutinosa* (nativo) and (b) *Aechmea blanchetiana* (restinga at Trancoso) in different size classes (surface area) showing the proportion of sites available and those occupied by *Eustiromastix nativo*.

Figure 3. (a) Density of *Vriesea neoglutinosa* bromeliads and (b) the proportion of plants occupied by *Eustiromastix nativo* in patches A1 and A2 in nativo.

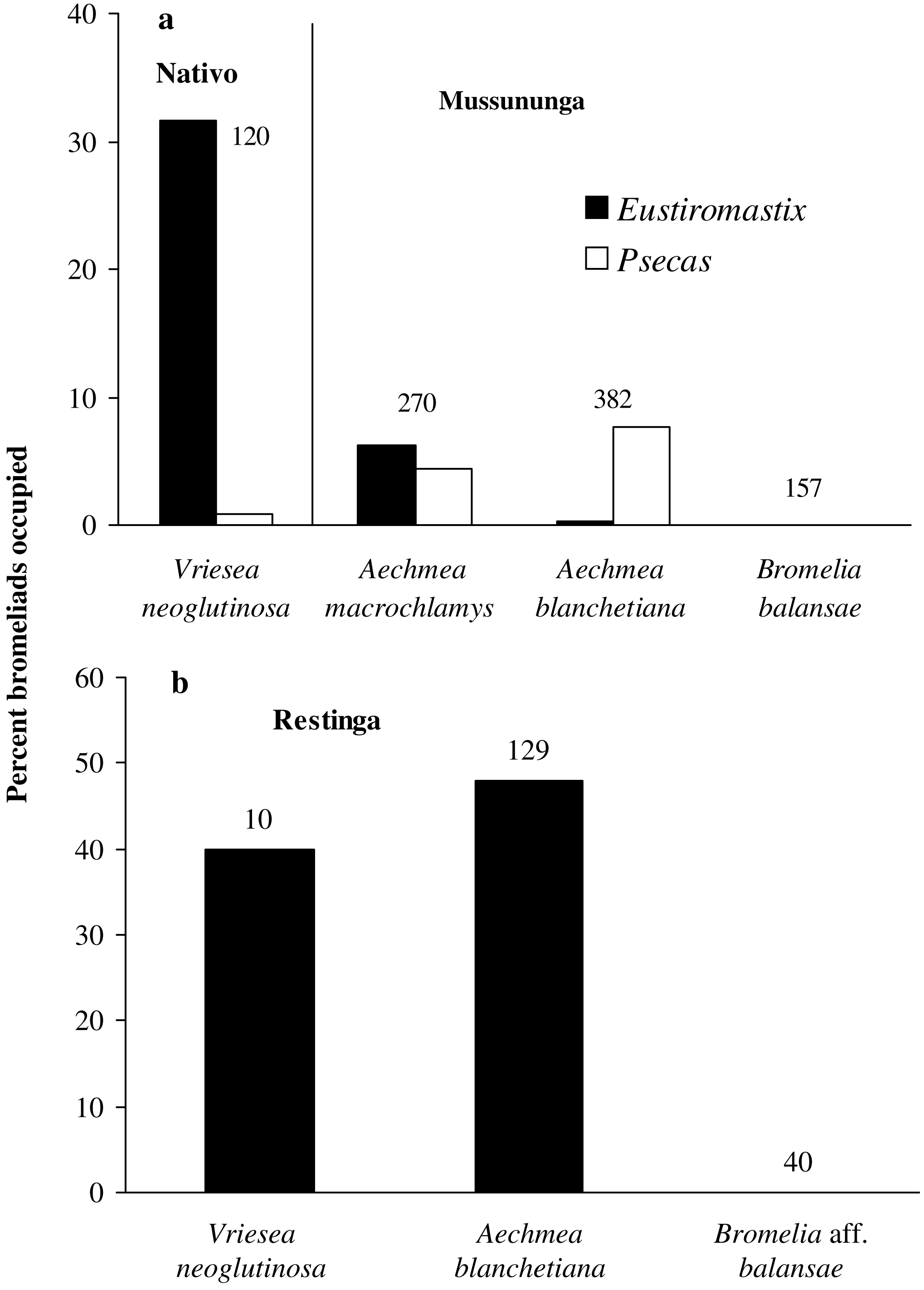
Percent bromeliads occupied
a
Nativo
Mussununga
■ Eustiromastix
□ Psecas
120
270
382
157
0
10
20
30
40
Vriesea neoglutinosa
Aechmea macrochlamys
Aechmea blanchetiana
Bromelia balansae
b
Restinga
10
129
40
0
10
20
30
40
50
60
Vriesea neoglutinosa
Aechmea blanchetiana
Bromelia aff. balansae

Fig. 1.

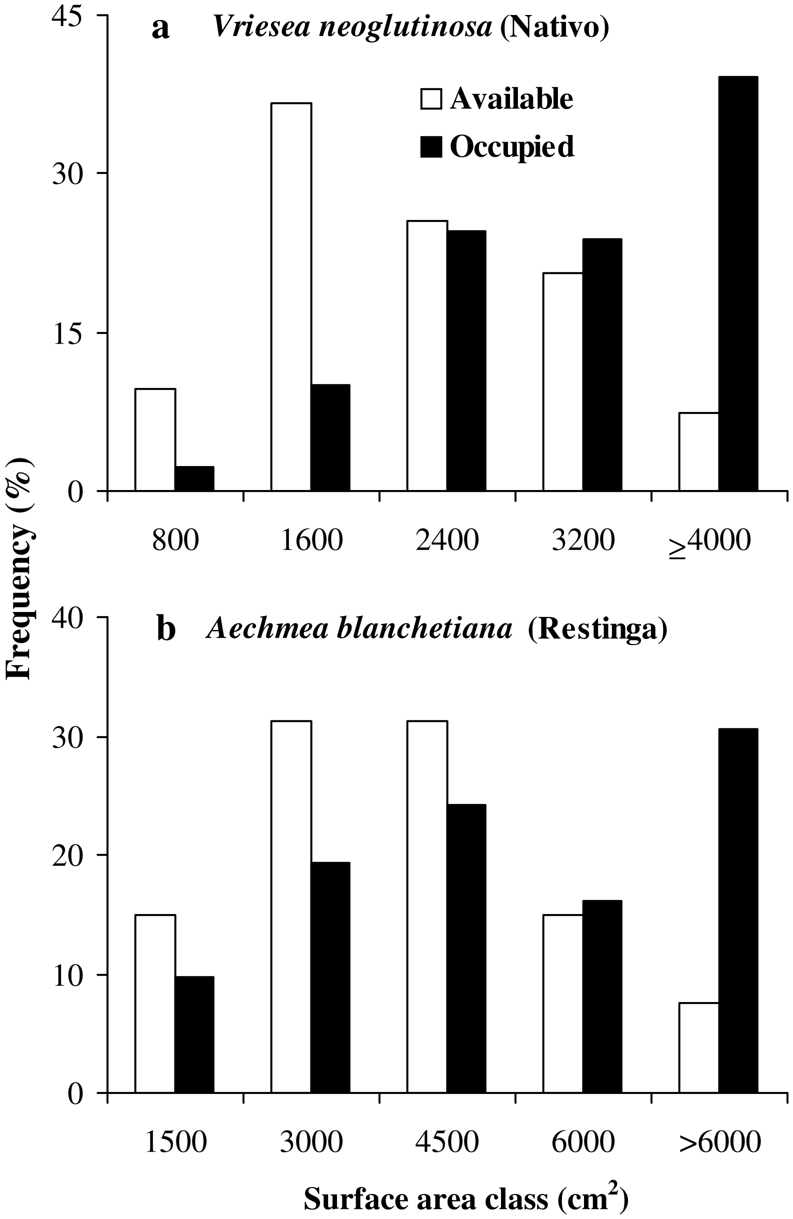
a *Vriesea neoglutinosa* (Nativo)
☐ Available
■ Occupied
45
30
15
0
800
1600
2400
3200
≥4000
Frequency (%)
b *Aechmea blanchetiana* (Restinga)
40
30
20
10
0
1500
3000
4500
6000
>6000
Surface area class (cm²)

Fig. 2.

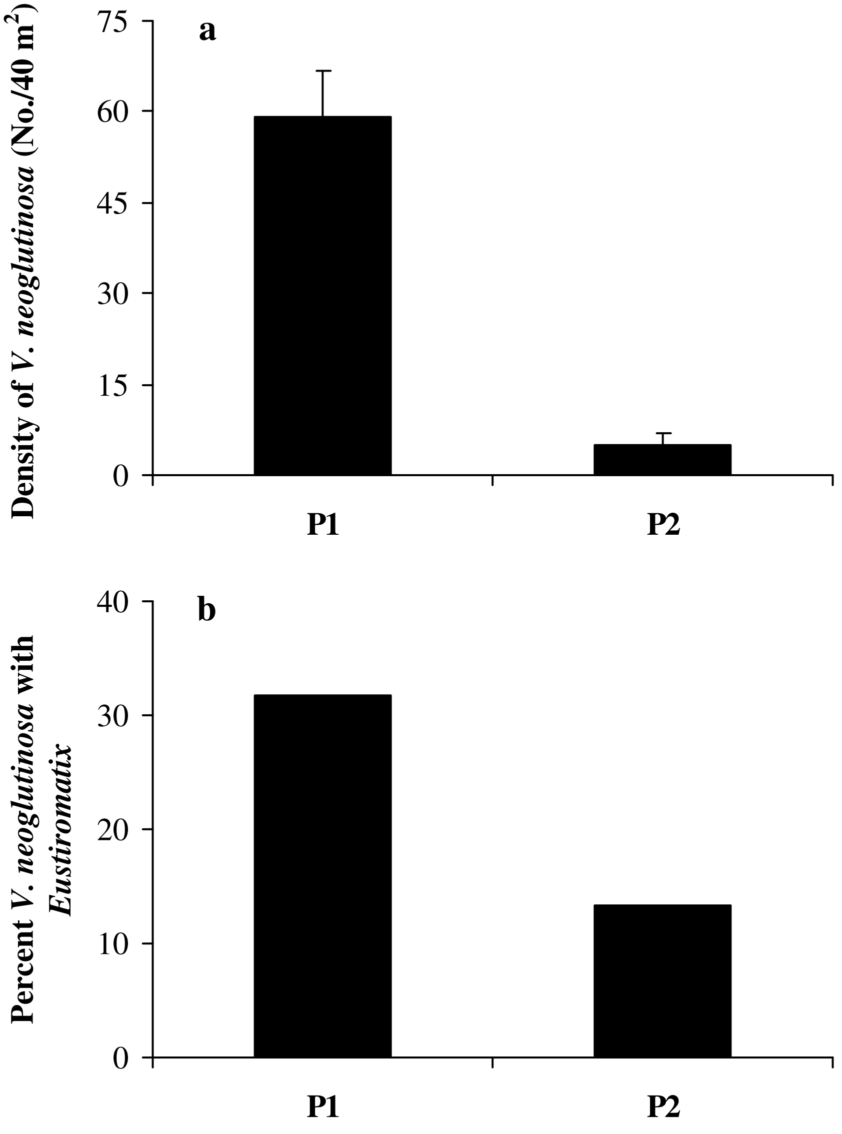
Density of *V. neoglutinosa* (No./40 m^2)
a
0
15
30
45
60
75
P1
P2
Percent *V. neoglutinosa* with *Eustiromatix*
b
0
10
20
30
40
P1
P2

Fig. 3.

Artigo 2

Manuscrito não publicado

Association of two *Coryphasia* species (Araneae, Salticidae) with tank-bromeliads in southeast Brazil: habitats and patterns of host plant use

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Running title: Association of *Coryphasia* with Bromeliaceae

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Abstract

Two allopatric species of *Coryphasia* (Salticidae) were found associated with Bromeliaceae in distinct phytophysiognomies (e.g., inselbergs, highland forests and "restingas") from south-east Brazil. In this study, we investigated whether these salticids were associated specifically with bromeliads, and whether they use particular bromeliad species and those with larger size, in distinct geographic regions. The *Coryphasia* species were rarely found outside bromeliads, occupied the larger bromeliad species among those available, and generally occurred more on bromeliads from open areas, such as inselbergs from mountain tops. We observed the two *Coryphasia* species submerging in the phytotelmata, a possible anti-predatory behavior. The patterns of spatial and microspatial distribution, as well as behaviors (e.g., submergence) of *Coryphasia* spp. were similar to other bromeliad-dwelling salticids, suggesting a convergence among these spiders to live on bromeliads.

Key-words: animal-plant interactions, Bromeliaceae, bromeliad-dweller, *Coryphasia*, jumping spider, microhabitat, Salticidae, specific association

Introduction

Plants of the family Bromeliaceae are almost exclusively neotropical and are frequently inhabited by a large variety of aquatic and terrestrial arthropods (Benzing 2000). Some spiders live associated specifically with bromeliads in South and Central America, and use these plants as foraging and mating sites, nurseries, and shelter against predation and climatic extremities (Barth *et al*. 1988a,b, Baurecht & Barth 1992, Dias *et al*. 2000, Rossa-Feres *et al*. 2000, Santos *et al*. 2002, Dias & Brescovit 2003, 2004, Romero &

Vasconcellos-Neto 2004, 2005a,b,c). All known species of the neotropical wandering spiders of the genus *Cupiennius* (Ctenidae), for example, are closely associated with particular plants, especially Bromeliaceae and Musaceae, on which they hide during the day and prey, mate, and molt during the night (Barth *et al*. 1988a). *Cupiennius salei* Keys. lives in close association with some bromeliad species (Barth & Seyfarth 1979, Barth *et al*. 1988a), and uses vibratory signals in their host plants to communicate during courtship (Barth *et al*. 1988b, Baurecht & Barth 1992). *Pachistopelma rufonigrum* Pocock (Theraphosidae) is also strictly associated with the tank-bromeliad *Hohenbergia ramageana* Mez. in northeastern Brazil, and probably use these plants as shelter against higher temperatures of the sandy soil and as nurseries (Dias *et al*. 2000, Santos *et al*. 2002, Dias & Brescovit 2003, 2004).

Recent studies have reported strict associations between jumping spiders and bromeliads (Rossa-Feres *et al*. 2000, Romero & Vasconcellos-Neto 2004, 2005a,b,c). For instance, *Psecas chapoda* (Peckham & Peckham) inhabits exclusively *Bromelia balansae* Mez. (Bromeliaceae), a terrestrial bromeliad that does not accumulate rain water, in several regions of Brazil, Paraguay and Bolivia (Höfer & Brescovit 1994, Rossa-Feres *et al*. 2000, Romero & Vasconcellos-Neto 2004, 2005a,b,c, G. Q. Romero, unpublished data). All its life cycle, including courtship behavior, mating, oviposition, and population recruitment of the immatures, occur on this plant (Rossa-Feres *et al*. 2000, Romero & Vasconcellos-Neto 2005b). While leaves are used as foraging and mating sites, the base of the rosettes is used as shelter and resting sites, and the center of the bromeliads is used as nurseries (Romero & Vasconcellos-Neto 2005a,c). *Eustiromastix nativo* Santos & Romero, *Psecas sumptuosus* (Perty) and an undescribed species of *Uspachus* (Salticidae) were also strictly associated with tank-bromeliads in southeastern and northeastern Brazil, and probably use bromeliads as shelters against predators and high temperatures, and as foraging and egg laying sites (Romero & Vasconcellos-Neto 2004). *Eustiromastix nativo* inhabited the larger bromeliads among those available, suggesting that it may evaluate, in fine details, the physical state of its microhabitats (Romero & Vasconcellos-Neto 2004).

Two undetermined *Coryphasia* species (*Coryphasia* sp. 1 and sp. 2, Salticidae) were found inhabiting some bromeliad species in inselbergs from mountain tops, highland forests and restingas in distinct geographic regions from southeastern Brazil. To understand these spider-plant relationships, we addressed the following questions: 1) Are *Coryphasia* spp. strictly associated with bromeliads? 2) Do these spiders occur more on bromeliads of larger size? 3) Do these spiders inhabit all the bromeliad species available with the same frequency? Some anti-predatory behaviors in these salticids were also described.

Methods

This study was done in four different regions from southeastern Brazil: in a rocky open site (inselberg) from a mountain top (elevation ~ 1900 m) and in an adjacent ombrophylous dense high-montane forest near Monte Verde city (22° 51'S, 46° 20'W), Minas Gerais state, in August to October 2003, December 2004 and April 2005; in an inselberg from Sugar Loaf ("Pão de Açúcar") (22° 57'S, 43° 09'W), Rio de Janeiro state, in April to May 2004; in a restinga (i.e., communities on sandy soil close to the shore) (Lacerda *et al*. 1984) from Parque Estadual da Ilha do Cardoso (25° 03'S, 47° 53'W), an island located on the coast of São Paulo state, in April 2005. Additional observations were done in a tropical semideciduous forest (elevation ~ 1000 m) in the Ecological Reserve of the Serra do Japi (23°11'S, 46°52'W), Jundiaí city, São Paulo state. *Coryphasia* sp. 1

inhabited bromeliads from Monte Verde and Serra do Japi, and *Coryphasia* sp. 2 inhabited bromeliads from Rio de Janeiro and Ilha do Cardoso.

All these species are certainly members of the genus *Coryphasia*, although we can not assign them to any described species because the almost chaotic state of Salticidae systematics in South America, especially regarding the subfamily Euophryinae. To permit the recognition of the species, this study includes illustrations of the genitalia for all the species (Fig. 1). Voucher specimens were deposited in the spider collection of Instituto Butantan, São Paulo, Brazil (reference numbers: *Coryphasia* sp. 1: IBSP xxx-xxx; *Coryphasia* sp. 2: IBSP xxx-xxx).

In Monte Verde, the bromeliads *Aechmea distichantha* Lem., *Nidularium innocentii* Lem. and *Vriesea bituminosa* Wawra were very common in the forest understories and were similar in leaf length and number of leaves (Table 1), but the former has a uniquely lithophytic habit, inhabiting open areas of the granitic rocks in inselbergs, and uniquely bearing conspicuous spines at their leaf edges. In Rio de Janeiro, the bromeliad species found were *Alcantarea glaziouana* (Lemaire) Leme and *Neoregelia cruenta* (R.Graham) L.B.Smith, and both inhabited only open areas of the granitic rocks at the inselberg (absent in forest), but only the latter had spines at their leaf edges. In Ilha do Cardoso, the bromeliad species found were *Quesnelia arvensis* (Vell.) Mez, *Aechmea nudicaulis* (L.) Griseb. and *Vriesea carinata* Wawra, and all occurred in shade environment (restinga understory); the first two species bear small spines and the latter has no spines in the leaf margins. In the Serra do Japi, the only terrestrial bromeliad available was *Bromelia antiacantha*. Of all these bromeliads, *B. antiacantha* was the only one that does not form phytotelmata.

We investigated whether *Coryphasia* spp. were strictly associated with bromeliads or whether they also occurred on other plants. For this, we inspected stems and leaves (abaxial and adaxial sides) of herbaceous plants and shrubs (non-bromeliads) up to 1.7 m total height, and branches and trunks of taller plants up to 1.7 m height, between 9:00 h and 16:00 h. Similar methods were also used in other studies (Romero & Vasconcellos-Neto 2004, 2005a). Plants from forest (n = 633) and from top of the mountain (n = 529) at Monte Verde were inspected along two random 150 m x 5 m transects, one in each site. We inspected non-bromeliaceous plants in the inselberg from Rio de Janeiro (n = 500) and in the restingas from Ilha do Cardoso (n = 320) along a random 150 m x 5 m transect and 70 m x 10 m transect, respectively.

To verify whether *Coryphasia* spp. inhabit larger plants, as do other bromeliad-dwelling jumping spiders (Romero & Vasconcellos-Neto 2004, 2005a,b), we sampled the first 70 rosettes of *Ae. distichantha* found, 30 of them occupied and 40 unoccupied by *Coryphasia* sp. 1 at the mountain top from Monte Verde. The same was done for *Coryphasia* sp. 2 at Rio de Janeiro, in 81 rosettes of *A. glaziouana* (41 occupied and 40 unoccupied by this species). We did not evaluate the preference of *Coryphasia* sp. 2 for plants of different size in Ilha do Cardoso. The size (surface area) of each rosette of *Ae. distichantha* was estimated as the product of the width (at base) x length of a leaf from median layer (node) multiplied by 0.5, since the leaves of this species assume a crudely triangular shape. The surface area of *A. glaziouana* was estimated by using the same procedures, but since the leaves of this bromeliad present a rectangular shape, the product of the length x width of a leaf from median layer was not multiplied by 0.5. The leaf area of each rosette was multiplied by the total number of green leaves to obtain an approximation of the total plant surface area. Only the bromeliads *Ae. distichantha* and *A. glaziouana* were used in these analyses because they were the most abundant in Monte Verde and Rio de Janeiro, respectively. The distribution of the relative frequencies of the rosette size classes available and those occupied by *Coryphasia* sp. 1 and sp. 2 were compared using G-test in contingency table (Sokal & Rohlf 1995).

To determine which bromeliad species *Coryphasia* sp. 1 inhabited with higher frequency in Monte Verde, we inspected the first 62 individuals found of *Ae. distichantha*, 111 of *N. innocentii* and 60 of *V. bituminosa* available in the forest, in a plot of 150 m x 20 m, and the first 70 individuals of *Ae. distichantha* at the mountain top, in a plot of 50 m x 30 m, for comparative analyses between habitats. We determined which bromeliad species *Coryphasia* sp. 2 occurred with higher frequency in Rio de Janeiro by inspecting the first 268 individuals of *A. glaziouana* and 88 individuals of *N. cruenta* available at the inselberg, in a plot of 150 m x 20 m. We also determined which bromeliad species *Coryphasia* sp. 2 inhabited with higher frequency in Ilha do Cardoso by inspecting 166 individuals of *Q. arvensis*, 48 individuals of *A. nudicaulis* and 55 individuals of *V. carinata* available in the restinga, along a 70 m x 10 m transect. For each bromeliad inspected, we recorded the presence/absence of the spiders. Amongst the bromeliads from Monte Verde forest and from Ilha do Cardoso, *Ae. distichantha*, *V. bituminosa*, *Q. arvensis* and *V. carinata* presented both terrestrial and epiphytic habits, but *N. innocentii* and *A. nudicaulis* were apparently only terrestrial and epiphyte, respectively. However, we examined only the bromeliads occurring in the ground and epiphytes up to 1.5 m in height. The bromeliads from Rio de Janeiro were all ground-dwellers.

We compared the occupancy of the spiders on different plant species by using a G-test. To calculate an expected value for the observed number (occupied by spiders) of plants of a certain bromeliad species, we multiplied the proportion of occurrence (abundance) of this bromeliad species by the total number of bromeliads occupied (of all plant species). This procedure was taken because the abundance of plants of each bromeliad species was variable. The data were presented as percentage of bromeliads occupied [(number of bromeliads occupied/total number of bromeliads)*100]. The p-values for multiple comparisons of the frequency of spiders on different bromeliad species (in Monte Verde) were adjusted using Bonferroni correction ($P = \alpha/n = 0.05/3 = 0.017$).

Results

Coryphasia spp. were not observed inhabiting other non-bromeliad plants in Monte Verde and Ilha do Cardoso. In Rio de Janeiro, five individuals of *Coryphasia* sp. 2 were found on five non-bromeliad plants. In these cases, the plants occupied by this species were shrubby and located up to 30 cm above thickets of the bromeliad *A. glaziouana*.

Coryphasia sp. 1 occurred non-randomly on individuals of *Ae. distichantha* of different sizes (surface area) in Monte Verde, with the highest frequency on larger bromeliads (contingency table, $G = 15.8$, 5 df, $P = 0.007$, Fig. 2). In contrast, in Rio de Janeiro *Coryphasia* sp. 2 tended to occur more on individuals of *A. glaziouana* of intermediate size (Fig. 2), but with statistical difference marginally non-significant (contingency table, $G = 10.0$, 5 df, $P = 0.075$). The surface area of *A. glaziouana* was larger than of *Ae. distichantha* (*A. glaziouana*: 9253.52 ± 670.08, $n = 81$; *Ae. distichantha*: 901.98 ± 56.28, $n = 70$; Mann-Whitney $U = 2524$, $P < 0.001$).

In the forest from Monte Verde, *Coryphasia* sp. 1 used the bromeliads available non-randomly ($G = 24.14$, 2 df, $P < 0.001$, Fig. 3), and occurred in higher frequency on *Ae. distichantha* relative to *N. innocentii* ($G = 24.13$, 1 df, $P < 0.001$) and on *V. bituminosa* relative to *N. innocentii* (G = 7.70, 1 df, P = 0.005), but inhabited with similar frequency on *Ae. distichantha* and *V. bituminosa* (G = 3.65, 1 df, P = 0.056). In this habitat, *V. bituminosa* was the largest bromeliad species (Table 1). The occupancy of this spider species was greater on *Ae. distichantha* from mountain top (open area) than on individuals of this bromeliad species from forest (G = 5.42, 1 df, P = 0.020, Fig. 3), despite the smaller size of *Ae. distichantha* from the open area compared to those from the forest (mountain top: 901.98 ± 56.28, n = 70; forest: 1445.55 ± 177.55, n = 17; Mann-Whitney U = 1022, P = 0.003). In Rio de Janeiro, *Coryphasia* sp. 2 occurred in higher frequency on *A. glaziouana* relative to *N. cruenta* (G = 30.22, 1 df, P < 0.001, Fig. 3). In this site, *A. glaziouana* was larger than *N. cruenta* (Table 1). In Ilha do Cardoso, the frequency of *Coryphasia* sp. 2 did not differ between the bromeliads *V. carinata* and *Q. arvensis* (G = 2.33, 1 df, P = 0.127), but this spider did not occur on *A. nudicaulis* (Fig. 3). This latter bromeliad was the smallest among those available in Ilha do Cardoso (Table 1). In Serra do Japi, we have observed a population of *Coryphasia* sp. 1 established on a thicket of *B. antiacantha* for more than 5 y.

In Monte Verde, we found 6 and 3 egg sacs of *Coryphasia* sp. 1 in the forest and at the mountain top, respectively, only on leaves of *Ae. distichantha*. In Serra do Japi we found one egg sac of this spider species on *B. antiacantha*. In Rio de Janeiro, we found five egg sacs of *Coryphasia* sp. 2 on only *A. glaziouana*. We did not find egg sacs on the bromeliads from Ilha do Cardoso.

Generally, when approached by an observer trying to capture them, *Coryphasia* sp. 1 and sp. 2 submerged in the water of the tank bromeliads (e.g., *Ae. distichantha* and *A. glaziouana*) by climbing down into the tank by clinging to the leaf. These individuals remained submerged for more than three minutes, and an air bubble seemed to surround them when submerged. We have not observed this submergence behavior in *Coryphasia* sp. 2 from Ilha do Cardoso. When on bromeliads that does not form phytotelmata (e.g., *B. antiacantha* from Serra do Japi), *Coryphasia* sp. 1 quickly fled to peripheral leaves and buried themselves in the bromeliad rosette.

Discussion

Our findings suggest that *Coryphasia* spp. were specifically associated with bromeliads, since they were rarely found on non-bromeliad plants. Moreover, *Coryphasia* spp. inhabited bromeliads from different geographic regions, suggesting a strong relationship of these spiders only with Bromeliaceae. Bromeliads may be a suitable microhabitat for salticids because their leaves form a complex tridimensional architecture that permits the adult spiders to forage and to take shelter against predators (Romero & Vasconcellos-Neto 2005a,c). Moreover, plants in rosette shape may be good sites for spiders to lay eggs and as nurseries for spiderlings (Santos *et al*. 2002, Romero & Vasconcellos-Neto 2004, 2005a,c). In addition, since several bromeliad-dwelling spiders live in open areas (e.g. Santos *et al*. 2002, Dias & Brescovit 2003, 2004, Romero & Vasconcellos-Neto 2004, 2005a,b, G.Q. Romero, unpublished data), where the ground (e.g., sandy or rocky habitats) is generally hot, during the day bromeliads may serve as shelter against high temperatures. According to our measurements, ground temperature at the inselberg in Monte Verde reached 50°C during the day (15:00h), while among the bromeliad leaves and into the phytotelmata the temperature was 27°C and 22°C, respectively. Therefore, the phytotelmata seems to function as a thermoregulation mechanism for the bromeliads and indirectly provide a suitable microclimate for the spiders (see also Dias & Brescovit 2004).

Coryphasia sp. 1 inhabited the larger rosettes of *Ae. distichantha* in Monte Verde, suggesting that these spiders may actively select their microhabitats based on host plant size. Romero & Vasconcellos-Neto (2004) reported that another bromeliad-dwelling salticid, *E. nativo*, presented similar microspatial distribution on two different bromeliad species, possibly because larger plants have a higher probability to be visited by insects due to their large surface area. However, *Coryphasia* sp. 2 apparently do not discriminates rosettes of *A. glaziouana* by their size in Rio de Janeiro. This bromeliad species was much larger than *Ae. distichantha*, and a variation in rosette size among large bromeliads may be difficult or unnecessary for *Coryphasia* sp. 2 to discriminate such a fine partitioning of its microhabitats.

In the forest from Monte Verde, *Coryphasia* sp. 1 occurred in higher frequency on *Ae. distichantha* and on *V. bituminosa* than on *N. innocentii*, and in Rio de Janeiro, *Coryphasia* sp. 2 occurred in higher frequency on *A. glaziouana* than on *N. cruenta*. *Vriesea bituminosa* and *A. glaziouana* were the largest bromeliads available in each region, and the spiders may select these plants because of their size. Despite *Ae. distichantha* being a small bromeliad, it was the only one in the forest that presented conspicuous spines at the edges of its leaves. These spines may provide protection against small vertebrates, as suggested by Romero & Vasconcellos-Neto (2005a,c) for other salticid-bromeliad system. *Coryphasia* sp. 2 also inhabited the largest bromeliads, *V. carinata* and *Q. arvensis*. However, it did not select for plants bearing spines in their leaf margins, in both areas of occurrence. This morphological trait in the plants from Rio de Janeiro (e.g., *N. cruenta*) and Ilha do Cardoso (e.g., *Q. arvensis*) may have no protective function for the *Coryphasia* species. Alternatively, this spider species may not select for host plants bearing spines in their leaf margins. *Coryphasia* sp. 2 did not occur on *A. nudicaulis* at Ilha do Cardoso. Besides this plant species being the smallest among those available, its leaves are strongly clustered forming a tube-like rosette. This architecture may be unsuitable for active hunters, such as Salticidae, that generally live and forage on tri-dimensional and open microhabitats (Romero & Vasconcellos-Neto 2004, 2005c). Alternatively, *Coryphasia* sp. 2 may avoid competition with females of the harvestman *Bourguyia albiornata*, which frequently uses *A. nudicaulis* in Ilha do Cardoso as oviposition site (Machado & Oliveira 2002).

Coryphasia sp. 1 occurred more frequently on bromeliads from mountain top (open area), where the ground is rocky and trees are scarce, than on forest-dwelling rosettes. Romero & Vasconcellos-Neto (2005a) reported similar dispersal pattern for *P. chapoda*, which occurred in higher frequency on rosettes of *B. balansae* from grasslands (open areas) than on rosettes from forest understories. Through manipulative experiments, Romero & Vasconcellos-Neto (2005c) demonstrated that dry leaves fallen from forest trees block the base (center) of *B. balansae* effectively impeding spider access to shelter and rest sites. In the present study, several forest-dwelling bromeliads had many dry leaves from trees into their rosettes. The dry leaves in rosettes can impede *Coryphasia* sp. 1 from accessing the water source (phytotelmata) and submerging in it.

The habit of *Coryphasia* spp. to submerge in the water of the phytotelmata can be an anti-predator adaptation to live on bromeliads. Similar submergence behavior was recorded for other two bromeliad-dwelling jumping spiders, *Eustiromastix nativo* and *Psecas sumptuosus* (Romero & Vasconcellos-Neto, unpublished data). These results suggest a convergence among these jumping spiders to live on tank-bromeliads.

In conclusion, *Coryphasia* spp. were specifically associated with bromeliads in different geographic regions, and inhabited the larger bromeliads among those available. Moreover, they apparently selected bromeliads from open areas. These spiders submerged in water of the bromeliad phytotelmata, as do other bromeliad-living jumping spiders, meaning a possible adaptation to inhabit tank-bromeliads.

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Table 1. Mean (± 1 SE in cm) of leaf length (LL), leaf base breadth (LB) and number of leaves (NL) for each bromeliad species at Monte Verde, Rio de Janeiro and Ilha do Cardoso. N = number of plants measured. Different letters indicate significant difference (ANOVA/Tukey post hoc test for data from Monte Verde and Ilha do Cardoso, and Student t-test for data from Rio de Janeiro).

Bromeliad species	LL	LB	NL	N
Monte Verde				
Aechmea distichantha	29.76±2.06 a	3.95±0.23 a	23.35±1.31 a	18
Nidularium innocentii	36.03±1.54 a	3.62±0.18 a	21.33±1.16 a	16
Vriesea bituminosa	36.53±3.55 a	7.47±0.33 b	19.12±1.33 a	17
Rio de Janeiro				
Alcantarea glaziouana	33.89±0.90 a	10.0±0.18 a	25.07±1.12 a	81
Neoregelia cruenta	20.12±1.01 b	7.04±0.24 b	16.64±0.93 b	25
Ilha do Cardoso				
Vriesea carinata	65.00±4.86 a	6.80±0.22 a	24.70±1.53 a	10
Quesnelia arvensis	40.60±2.00 b	6.02±0.20 b	26.30±2.22 a	10
Aechmea nudicaulis	44.40±2.70 b	5.27±0.18 c	6.80±0.25 b	10

Figure captions

Fig. 1. *Coryphasia* spp. (A-E) *Coryphasia* sp.1. (A) Male palp, ventral view. (B) Ditto, lateral. (C) Female epigynum, ventral view. (D) Female internal genitalia, dorsal view. (E) Ditto, ventral. (F-J) *Coryphasia* sp.2. (F) Male palp, ventral view. (G) Ditto, lateral. (H) Female epigynum, ventral view. (I) Female internal genitalia, dorsal view. (J) Ditto, ventral. Scale lines: 0.5 mm.

Fig. 2. Relative frequency of *Aechmea distichantha* (from Monte Verde) and of *Alcantarea glaziouana* (from Rio de Janeiro) in different size classes occupied respectively by *Coryphasia* sp. 1 and *Coryphasia* sp. 2 (black bars) and available (open bars).

Fig. 3. Percentage of the bromeliad species occupied by *Coryphasia* sp. 1 in the inselberg (left of the vertical line) and forest (right of the vertical line) from Monte Verde, and by *Coryphasia* sp. 2 in the inselberg from Rio de Janeiro and restinga from Ilha do Cardoso. The number of plants inspected is indicated above the bars.

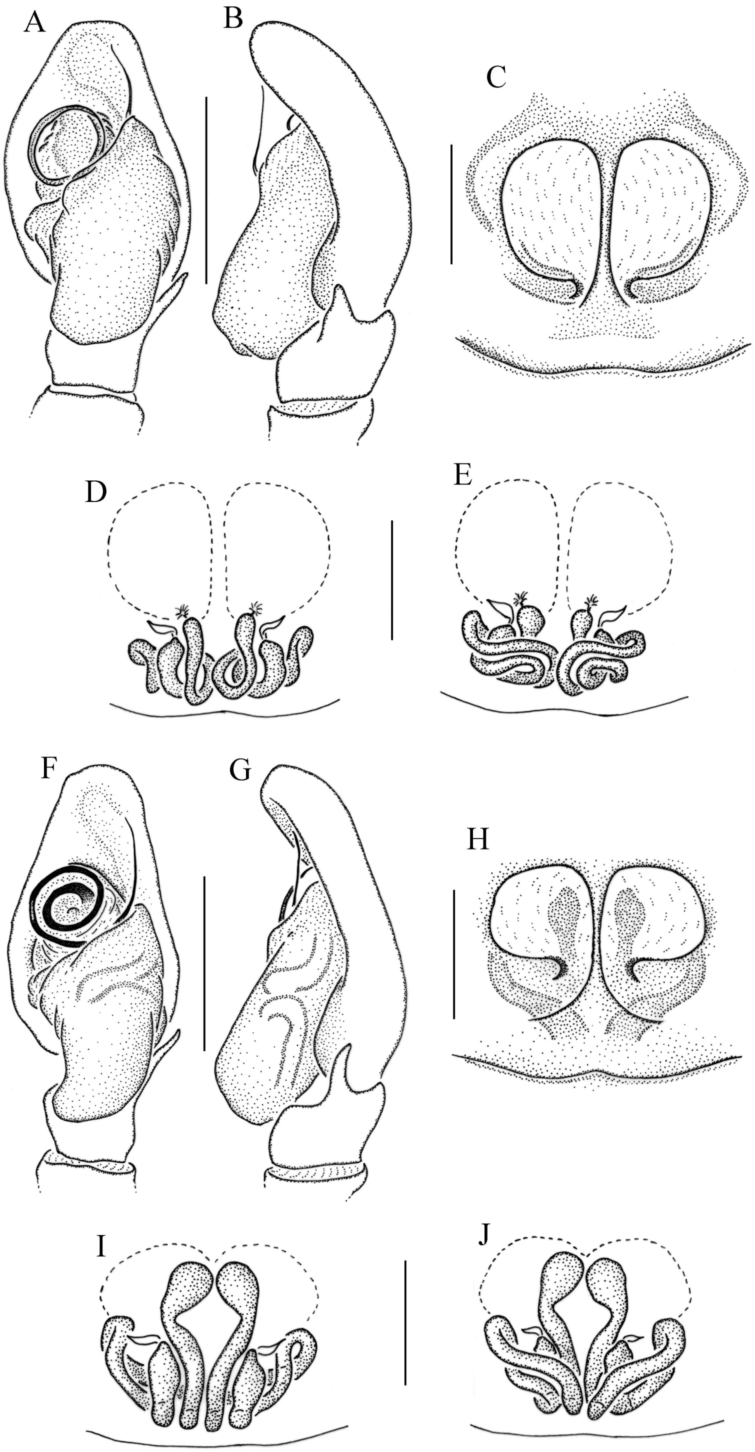


Fig. 1

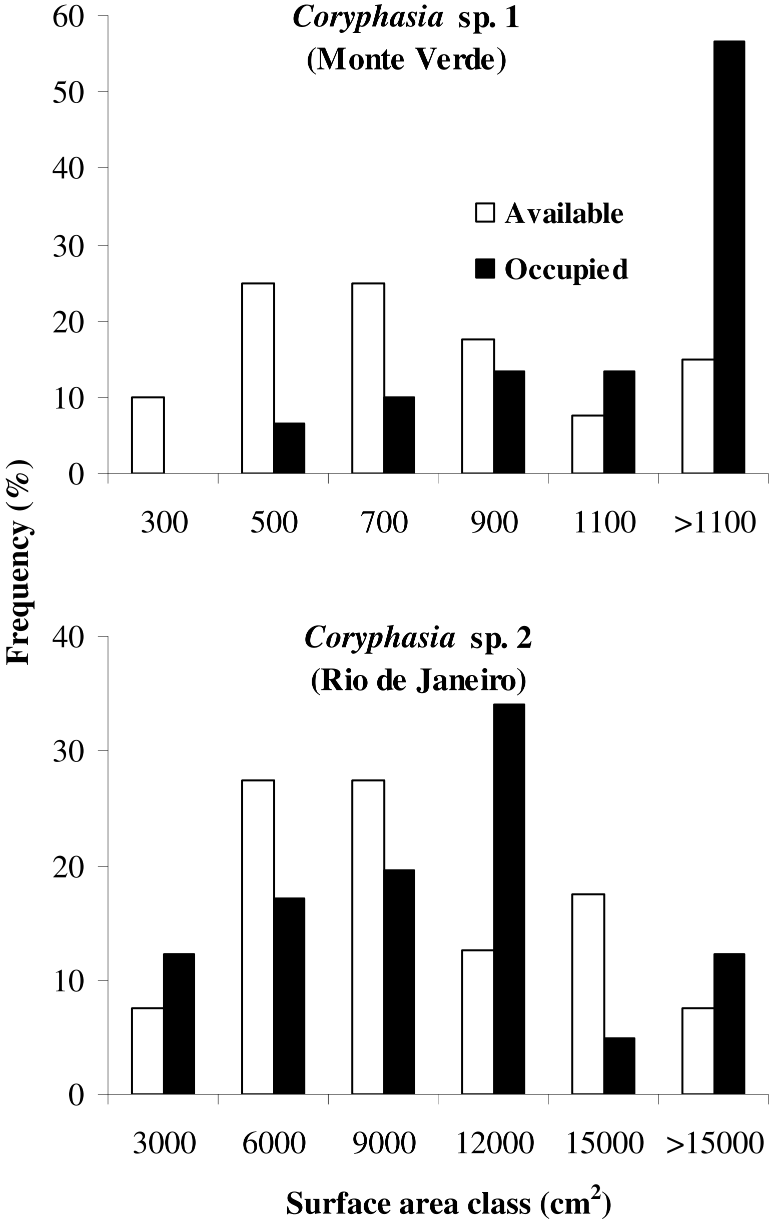
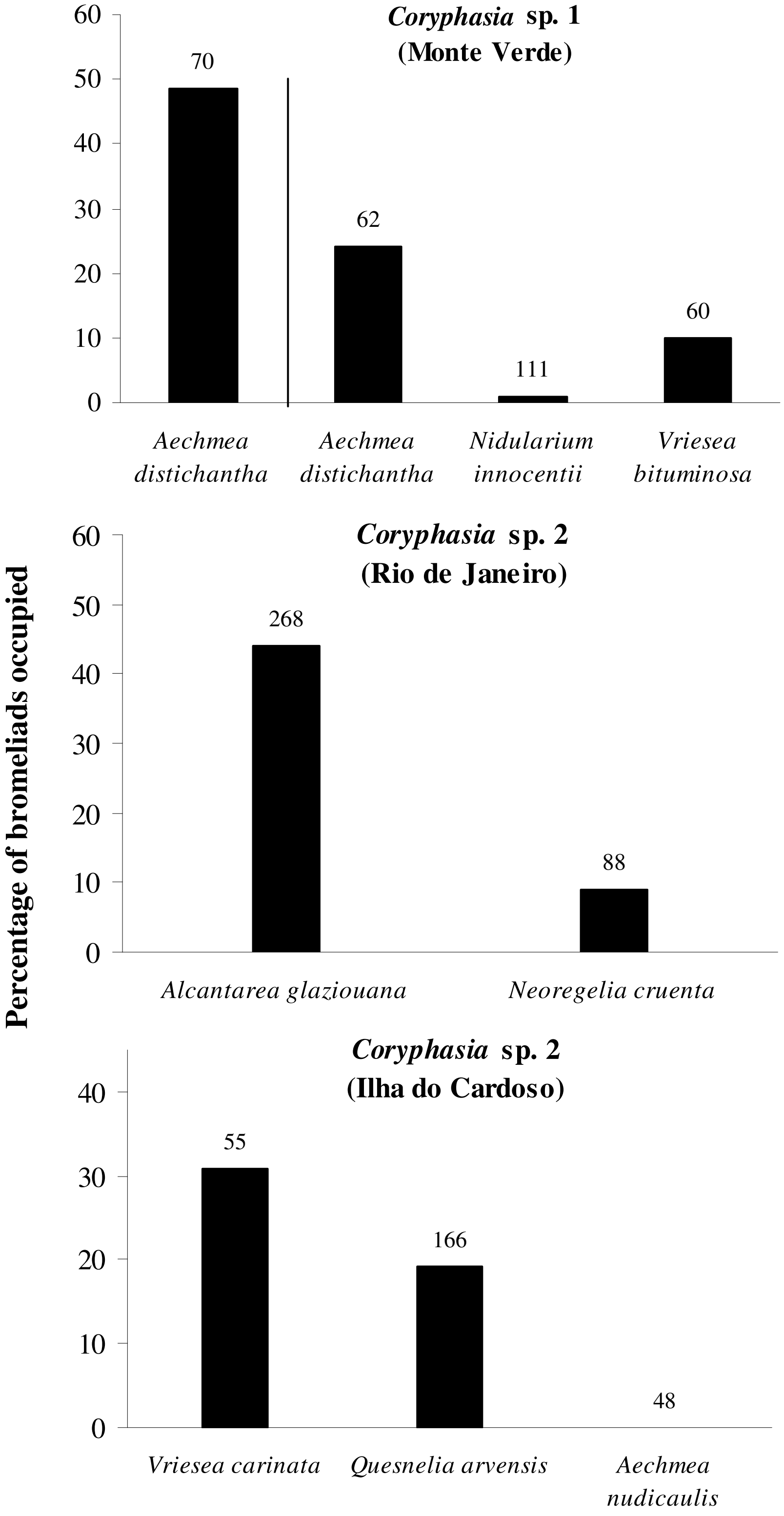

Coryphasia sp. 1
(Monte Verde)
☐ Available
■ Occupied
60
50
40
30
20
10
0
300
500
700
900
1100
>1100
Frequency (%)
Coryphasia sp. 2
(Rio de Janeiro)
40
30
20
10
0
3000
6000
9000
12000
15000
>15000
Surface area class (cm²)

Fig. 2



Percentage of bromeliads occupied
Coryphasia sp. 1
(Monte Verde)
60
50
40
30
20
10
0
70
62
111
60
Aechmea distichantha
Aechmea distichantha
Nidularium innocentii
Vriesea bituminosa
Coryphasia sp. 2
(Rio de Janeiro)
60
50
40
30
20
10
0
268
88
Alcantarea glaziouana
Neoregelia cruenta
Coryphasia sp. 2
(Ilha do Cardoso)
40
30
20
10
0
55
166
48
Vriesea carinata
Quesnelia arvensis
Aechmea nudicaulis

Fig. 3

Psecas chapoda sobre *Bromelia balansae* em Dois Córregos, SP. (A) fêmea sobre ovissaco, (B) macho adulto, (C) acasalamento, (D) fêmea e ovissaco.

Artigo 3

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

SPATIAL DISTRIBUTION AND MICROHABITAT PREFERENCE OF *PSECAS CHAPODA* (PECKHAM & PECKHAM) (ARANEAE, SALTICIDAE)

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ABSTRACT. Although spiders generally do not have a strong association with the plants on which they live, the jumping spider *Psecas chapoda* inhabits and breeds on *Bromelia balansae* (Bromeliaceae). To understand the relationship between *Psecas chapoda* and *Bromelia balansae*, we investigated whether the type of habitat (forest or grassland), the size of the bromeliad and the inflorescence of the host plants affected the preference and/or density of *P. chapoda*. We also examined how spiders of different ages and their eggsacs were distributed on the leaf layers of the rosette of host plants and whether *P. chapoda* used other plants in addition to *B. balanasae*. *Psecas chapoda* occurred with higher frequency on bromeliads in grasslands to those in forest. In grassland, larger bromeliads had more spiders, but this was not true of bromeliads in the forest. This spider avoided bromeliads with inflorescence. Most of the spiderlings (70%) occurred in the central layer of the rosette leaves, and their distribution pattern suggested that they sought shelter to protect themselves from desiccation or cannibalism, both of which are commonly observed in this species. Older spiders, as well as females without eggsacs, occurred in the external layers whereas 90% of the females with eggsacs occurred close to the central layers. Deposition of the eggsacs near the center of the rosette can allow the spiderlings to reach their shelter rapidly and to be less exposed to desiccation and cannibalism. The not detection of *P. chapoda* on non-bromeliad plants, and the stereotyped behaviors on the host-plant suggest that this jumping spider was strongly associated with *B. balansae*.

Keywords: Animal-plant interaction, habitat selection, microhabitat, plant architecture, Salticidae

In contrast to host-specific herbivorous insects (Schoonhoven et al. 1998), spiders generally do not have a strong association with the plants on which they occur. However, some spider species inhabit and breed on specific plants and interact indirectly with their hosts (Louda 1982; Figueira & Vasconcellos-Neto 1991, 1993; Rossa-Feres et al. 2000; Romero & Vasconcellos-Neto in press a). Why some spiders choose specific plants and how the occurrence of such spiders affects the organization of spider communities are important aspects in understanding the community structure on a given host plant and in elucidating the direct and indirect interactions within and among species (Abraham 1983; Uetz 1991). The components of habitat reported to influence the numbers and types of spiders include the abundance and richness of prey (Riechert & Tracy 1975; Waldorf 1976; Rypstra 1983; Miller & Drawer 1984; Schmalhofer 2001), the availability of extra-floral nectarines as a food source and as foraging sites (Ruhren & Handel 1999), the availability or density of sites for constructing webs (Lubin 1978; Rypstra 1983; Greenstone 1984; Herberstein 1997; Figueira & Vasconcellos-Neto 1991), the availability of foraging sites (Scheidler 1990; Romero 2001; Schmalhofer 2001; Romero & Vasconcellos-Neto in press b), the spatial distribution of web and foraging sites (Greenquist & Rovner 1976; Robinson 1981; Louda 1982) and the availability of sites for shelter (Riechert & Tracy 1975; Gunnarsson 1990, 1996) and breeding (Smith 2000).

The jumping spider *Psecas chapoda* (Peckham & Peckham, 1894) (Salticidae), previously identified as *P. viridipurpureus* Simon, 1901 by Rossa-Feres et al. (2000), is commonly found on *Bromelia balansae* Mez. (Bromeliaceae) and has an apparently host-specific distribution. Whereas bromeliads generally store rainwater in their rosettes, *Bromelia balansae* is an exception in that it does not accumulate rain water. *Psecas* *chapoda* spends its entire reproductive cycle: courtship, mating, ovisac formation and populational recruitment of the young spiders on this plant (Rossa-Feres et al. 2000). Females produce 1-3 eggsacs on the concave side of the central region of the leaves. The eggsacs are enveloped with a plain silk cover and are spun at the edge of each leaf. Since females remain under this cover and on the eggsacs (Fig. 1) (Rossa-Feres et al. 2000), there may be maternal care of the offspring.

In this study, we examined the spatial and microspatial patterns of *P. chapoda* on *B. balansae* and investigated the factors affecting this distribution. Specifically, we assessed whether the type of habitat (forest or grassland) and the size and architecture (absence vs. presence of inflorescences) of the bromeliad affected the density of *P.chapoda*. We also determined whether spiders of different ages and the eggsacs were randomly distributed among the leaf layers of the rosette, and whether *P. chapoda* was associated exclusively with *B. balansae*.

METHODS

This work was done in a fragment of semideciduous forest (250 m x 60 m) and in an adjacent grassland area along the margin of a dam, in the city of Dois Córregos (22º 21' S, 48º 22' W), São Paulo state, southwestern Brazil, from July 1998 - May 2000 and in March and April 2002. Only *Bromelia balansae*, a ground-dwelling bromeliad (Figs. 2-4), occurs in the study area.

Habitat preference. – Habitat preference was determined by recording the number of *P. chapoda* on *B. balansae* growing in the forest and in the grassland. Observations were made in the cold-dry season (July 1998), at the beginning of the rainy season (October

1998), in the hot-rainy season (February 1999) and at the end of the rainy season (April 1999), along two parallel 250m transects in the forest and grassland (one each). The two transects were at least 20-30 m apart, and 37-53 stalks of *B. balansae* in the forest and 75-103 stalks in the grassland were randomly chosen in each season. The spider density per bromeliad stalk was compared between the forest and grassland transects and among the four seasons using two-way ANOVA. Since the occurrence of the spiders may be skewed by the density of bromeliads, the number of plants growing at 10 m intervals in 100 m x 6 m transects of forest and grassland was estimated to determine if there were variations in density between sites. Since the preference for bromeliads was affected by the presence of inflorescence, only bromeliads without inflorescence were included in the analysis (see item 3 below).

Influence of host plant size on the microhabitat preference. – To examine the preference of spiders for host plants of different sizes, the relationship between the bromeliad surface area and the number of *P. chapoda* was examined for bromeliads in grassland, at the forest margin and within the forest. The bromeliads (50-82 in grassland, 16-27 at the forest margin and 31-53 within the forest) were observed bimonthly from July 1998 - July 1999. The bromeliads were randomly chosen in each sample period. Bromeliads growing under tree branches and which received incident solar light at any time of the day were considered to occur in the forest margin. The total surface area was estimated by multiplying the surface area of one leaf by the total number of green leaves on each bromeliad. The leaf surface area was estimated using the formula: length (L) x breadth (B) of a leaf from the middle layer of the rosette, chosen at random, x 1/2. Linear regression analysis was used to assess the relationship between surface area and the number of spiders. Student t-test was used to compare the bromeliad surface area between grassland and forest.

Influence of inflorescence on spider density. – The relationship between *B. balansae* inflorescence and spider density was examined by comparing the density of spiders on grassland *B. balansae* with and without inflorescence (Figs. 2-4). The observations were made in December 1998 and 1999 because almost all of the *B. balansae* at the study sites bloomed in this season. The results were analysed using the G-test.

Preference for leaf layers. – *Bromelia balansae* has several leaf layers in the rosette (Figs. 2, 3). Since preliminary observations showed that *P. chapoda* was distributed in different layers of the rosette according to the spiders' age, the distribution patterns of spiders of different ages were determined by examining 24-64 grassland bromeliads with at least five leaf layers. The observations were made bimonthly, from November 1999 - May 2000. The bimonthly interval of observations was determined to avoid data dependence (i.e., temporal pseudoreplication, Hurlbert 1984), since spiders change instars by molting and the eggsacs are constructed and abandoned in approximately one month (Rossa-Feres et al. 2000; G. Q. Romero, pers. obs.). Age-specific patterns of spots and coloration were used to classify *P. chapoda* as spiderlings (3rd instar), young (4th and 5th instars), and juvenile males (up to 1.1 cm in body length) or females (6th instar). Although sex-specific patterns of spots and coloration are also useful for discriminating subadult and adult stages, subadult and adult females with the same spot and coloration patterns and of similar size (up to 1.6 cm in body length) are difficult to distinguish in the field. In addition, the number of subadult males is extremely small. For these reasons, we created two additional groups, namely subadult (7th instar) + adult females (8th instar) and adult males (8th instar) (Rossa-Feres et al. 2000; G. Q. Romero pers. obs.). In the subadult and adult female class, the adult females with eggsacs were distinguished from subadult and adult females without eggsacs. The distributions of the five developmental stages above and those of subadult and adult females with and without eggsacs were analyzed using the G-test.

Selectivity of *P. chapoda* for the host plant. – The selectivity of *P. chapoda* for *B. balansae* was examined in March and April 2002, a period of high spider density, by the following three methods: 1) Direct observation – searching for spiders, silk shelters and abandoned eggsacs on 590 non-bromeliad plants belonging to the families Asteraceae, Fabaceae, Solanaceae, Asclepiadaceae, Lauraceae and several grasses. The plants examined were 10-170 cm tall and grew at least 3 m away from *B. balansae*. At each observation, we examined the abaxial and adaxial sides of leaves and branches. 2) Beating or shaking the plants with a stick. The spiders were collected on a beating tray, essentially a cloth-covered frame that sloped slightly towards the center (Southwood 1978). All of the spiders dropping off non-bromeliad plants (up to 170 cm tall) were collected. Fifty plants were sampled in grassland, 50 at the forest margin and 50 within the forest. Five beats per sample (plant) were done between 01:00h - 04:00h p.m. 3) Pitfall traps – 30 pitfall traps (10 cm in diameter and 15 cm deep) containing 75% ethanol were placed among individuals (0.4-1.5 cm) of *B. balansae*. The spiders were collected five days after. Voucher specimens of *P. chapoda* were deposited in the Laboratório de Artrópodes Peçonhentos, Instituto Butantan, São Paulo.

RESULTS

Habitat preference. – The average number of *P. chapoda* on *B. balansae* was significantly greater in grassland than in forest (two-way ANOVA, $F_{1,534} = 123.67$, $P <$

0.0001, Fig. 5). The average number of *P. chapoda* on *B. balansae* also changed seasonally (two-way ANOVA, $F_{3,534} = 2.89$, $P = 0.035$) and was lower in the hot, rainy season (Fig. 5). The interaction between the factors habitat and seasonality was significant ($F_{3,534} = 2.82$, $P = 0.038$). There was no difference between the density of bromeliads in grassland and forest (T-test, $t = -0.46$, 18 df, $P = 0.648$).

Influence of host plant size on the microhabitat preference. – There were positive, significant relationships between bromeliad surface area (size) and number of spiders inhabiting the plant, in the grassland and forest margins (Table 1). Despite of the bromeliads from forest be bigger than the bromeliads from grassland (data from July 1998; forest: 9649.0 cm^2 ± 1256.2 (SE), grassland: 4609.5 ± 470.6 (SE); $t = -4.53$, 154 df, $P < 0.001$), there were no relationships between plant size and number of spiders in the forest (Table 1). Up to 21 spiders were seen on a single plant in the grassland area, whereas a maximum of 3 spiders was seen on bromeliads in the forest.

Influence of inflorescence on spider density. – Among bromeliads with no inflorescence, 79% and 90% were occupied by *P. chapoda* in 1998 and 1999, respectively. In contrast, for bromeliads with inflorescences, only 17% and 13% were used by *P. chapoda* in 1998 and 1999, respectively. The percentage of bromeliads used by *P. chapoda* was significantly different between stalks with and without inflorescences (Fig. 6).

Preference for leaf layers. – Spiderlings occurred only in the first three central layers of the rosettes of *B. balansae.* Their distribution among the three layers was not random ($G = 30.60$, 2 df, $P < 0.0001$), and more spiderlings (70%) occupied the first layer in the center of the plant (Fig. 7). Although young spiders occurred on plants with five or more layers, 50% of this age interval was observed in the second layer ($G = 114.90$, 4 df, P

< 0.0001, Fig. 8). Juvenile males and females were not found in the first layer and used the other layers randomly (*G* = 5.03, 3 df, *P* = 0.170, Fig. 9). The random use of all layers except for the first one was also observed for adult males (*G* = 1.80, 3 df, *P* = 0.615, Fig. 10). In the case of subadult and adult females, more than 40% occurred in the third layer (*G* = 43.20, 4 df, *P* < 0.0001, Fig. 11). The distribution patterns of spiders among the leaf layers was different between adult females with eggsacs and subadult and adult females without eggsacs. More than 90% of the females with eggsacs occupied the second and the third layers (*G* = 18.70, 2 df, *P* < 0.0001), while the subadult and adult females without eggsacs occurred in the third, fourth and fifth layers with higher frequencies (*G* = 22.65, 4 df, *P* = 0.0001, Fig. 12). Only one adult or subadult female occupied the first layer.

Selectivity of *P. chapoda* for the host plant. – No individuals of *P. chapoda* or their vestiges (silk shelters and abandoned eggsacs) were found on 590 non-bromeliad plants close to *B. balansae* individuals. Although many spiders (~400 individuals) belonging to several families, including 6-7 Salticidae species, were collected by beating non-bromeliad plants and in pitfall traps on the ground between the stalks of *B balanasae*, no *P. chapoda* were found. In three years of observations, only three adult *P. chapoda* males were observed on the ground and one young was seen on a gramineous leaf close to *B. balansae* in grassland.

DISCUSSION

Although several studies have shown that spiders of the family Salticidae may select certain microhabitats (Crane 1949; Richman & Whitcomb 1980; Jackson 1986; Cutler 1992; Cutler & Jennings 1992; Johnson 1995; Jackson & Li 1997; Taylor 1998), the distribution of *P. chapoda* on *B. balansae* and the absence of this species on non-bromeliad plants and in pitfall traps around bromeliads suggested a strong relationship between *P. chapoda* and *B. balansae*. The courtship, mating, deposition of eggsacs and populational recruitment of *P. chapoda* occur on *B. balansae*. *Psecas chapoda* also used *B. balansae* throughout the year at Sao José do Rio Preto (SP), about 200 km from the present study site (Rossa-Feres et al. 2000). Moreover, this spider species was collected and photographed (female) on *B. balansae* in Beni, Bolivia (Höfer & Brescovit 1994: picture 2a; H. Höfer, pers. comm.). In addition, *P. chapoda* was observed on *B. balansae* in 26 cities of three Brazilian states and in one locality of Paraguay (G.Q. Romero, unpubl. data). Thus, *P. chapoda* seems to be strictly associated with *B. balansae* in a large geographic range.

Our results show that *P. chapoda* preferred bromeliads in grassland to those in forest, and that bigger bromeliads were preferred more in grassland, whereas such a relationship between plant size and the average number of spiders was not observed in forest bromeliads. When the bromeliads are approached by an observer, *P. chapoda* on the leaf layers quickly jump towards the bottom of the rosette in a stereotyped jumping behaviour (G. Q. Romero, personal observation). The internal base of the rosette of bromeliads serves as a refuge and shelter from desiccation, as well as a resting place (G. Q. Romero, personal observation). In forest, the bromeliads receive a large number of dry leaves from trees growing nearby and these leaves form a compact humic mass that fills completely the internal base of the bromeliad rosettes, regardless of the difference in size. Since a large quantity of dry leaves at the bottom of the rosette hampers the use of this microhabitat, *P. chapoda* appears to prefer grassland bromeliads which gather little or no dry leaves compared to forest bromeliads.

Larger bromeliads had more individuals of *P. chapoda*. Larger plants have larger surface area available for foraging and many leaf layers in their rosettes for shelter, which can support more spiders. Generally, populations of spiders that inhabit larger bromeliads consist of one adult male, one or two adult females frequently with eggsacs and several young and spiderlings, probably offspring of these resident females. In contrast, little, peripheral bromeliads are frequently occupied by young, juveniles and subadult spiders (G.Q. Romero, pers. obs.). Adult females probably choice larger bromeliads to obtain more food and shelter for their offspring, decreasing the probability of intraspecific competition and/or cannibalism among them. Since salticid jumping spiders have good eyesight (Foelix 1982; Foster 1982), they can obtain more food on larger leaves. Figueira & Vasconcellos-Neto (1993) showed a strong relationship between the size of the *Paepalanthus bromelioides* (Eriocaulaceae) rosette and prey availability, and between the size of the *P. bromelioides* rosette and the weight and/or reproductive success of *Latrodectus geometricus* Koch, 1841 (Theridiidae). According to these authors, larger plants offered a larger amount of prey for *Latrodectus* females so that females grew rapidly and produced more eggs.

In addition to the size of *B. balansae,* the presence of inflorescence also affected the abundance of *P. chapoda* since almost all spiders occurred on bromeliads without inflorescence. During the reproductive period of *B. balansae*, the green color of the central parts (leaves) of the rosette changes to red prior to inflorescence blooming. At the same time, the leaves fold back and extend parallel to the ground (Fig. 4) to expose the flowers to pollinators. These changes alter the plant architecture from a conical tridimensional configuration to a flattened, almost bidimensional one. Since the leaves do not touch each other even at this time because of the geometric conformation of the plant, the surface area of the leaves of bromeliads remains constant, even after the blooming season. However, the change in plant architecture affects the availability of shelter and breeding sites, and the spiders are exposed to external factors such as predation and climatic conditions. Some jumping spiders are able to find and catch prey in tridimensional and topographically complex environments (Hill 1979; Tarsitano & Andrew 1999). If *P. chapoda* also prefers bromeliads with a tridimensional arrangement, the preference for bromeliads without inflorescence could be explained by differences in the shelter and breeding sites and by architectural changes in the host plants.

Although most arthropods in the tropics show peak numbers in the hot, rainy season (see Wolda 1988), *P. chapoda* was more abundant in the cold, dry season and at the end of the rainy season. Many grass species around bromeliads grow rapidly in the rainy season and may cover part of the bromeliads. Although additional studies on the causes of the high density of *P. chapoda* in the cold, dry season are necessary, the abundance of grasses may affect the availability of food for the spiders, and may influence the amount of contact between male and female spiders, as well as the colonization of bromeliads.

In some spider species there are differences in the choice of microhabitat among adults and immatures in order to facilitate prey capture and to avoid predation (Edgar 1971). It is possible that *P. chapoda* may show age-specific use of bromeliads.

Approximately 70% of the *P. chapoda* spiderlings occurred in the first central layer of the *B. balansae* rosette. Since the leaves extend vertically in the first layer, they overlap each other to form a cylinder of small diameter. Small spiderlings can use this microhabitat to shelter from desiccation and/or cannibalism by larger spiders. Young spiders, one or two instars older than the spiderlings, and which still need a place to shelter, occurred more frequently in the second layer of the rosette because of the difficulty in reaching the first layer, that has very narrow and clumped leaves. Juvenile males and females of a similar size to the adults were generally restricted to outer layers.

The value of the central rosette as a shelter was also suggested by the different distribution of females with and without eggsacs. Almost all of the females with eggsacs (90%) occurred between the second and third layers, whereas females without eggsacs were more common in the outer layers (Fig. 12). When females with eggsacs remained at the center of the rosette, the hatched spiderlings easily reached the first layers and the probability of cannibalism was reduced. Several studies have shown that during oviposition, the females of insects choose plants that enhance the performance of their offspring (see Schoonhoven et al. 1998). Females of *P. chapoda* remained over their eggsacs (Rossa-Feres et al. 2000), indicating that there was more than one type of maternal investment in offspring in this spider species. According to Richman & Jackson (1992), such maternal behavior is very common, if not universal, in the Salticidae, and presumably deters the predators and parasitoids of eggs. These results suggest that the distance from the ovisac to the center of the bromeliad may influence the type of maternal behavior seen. Desiccation and cannibalism can represent selective pressures that influence the choice of breeding sites by females and this may affect the survival of the offspring after leaving the nest.

In conclusion, *P. chapoda* was associated with *B. balansae* from grassland. This spider occurred in very low frequency on bromeliads from forest and those from grassland with presence of inflorescence. The specific behaviors of *P. chapoda* on the plant and the absence of detection of this species on non-bromeliad plants suggest a strict association between *P. chapoda* and *B. balansae*.

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Table 1.–Linear regressions of the relationship between the bromeliad size (surface area) and individuals number of *Psecas chapoda* in the grassland, forest margins and into the forest, in different seasons.

	Places	Equations	n	r^2	*F*	*P*
1998						
	Grassland	Y = 0.00033 X + 1.44	82	0.51	84.67	<0.001
Jul	Margin	Y = 0.000102 X + 0.94	21	0.27	7.06	0.016
	Forest	Y = 0.0000013 X + 0.63	53	0.0003	0.02	0.899
	Grassland	Y = 0.00011 X + 1.11	76	0.09	7.22	0.009
Sep	Margin	Y = 0.000031 X + 0.86	22	0.04	0.77	0.390
	Forest	Y = 0.0000006 X + 0.28	53	0.0001	0.001	0.932
	Grassland	Y = 0.00045 X + 1.27	74	0.08	6.70	0.012
Nov	Margin	Y = 0.000084 X + 0.74	27	0.06	1.51	0.231
	Forest	Y = 0.000002 X + 0.31	48	0.001	0.06	0.806
1999						
	Grassland	Y = 0.00055 X + 0.89	67	0.22	18.64	<0.001
Jan	Margin	Y = 0.000047 X + 1.92	18	0.01	0.25	0.623
	Forest	Y = 0.000002 X – 0.56	43	0.0009	0.04	0.849
	Grassland	Y = 0.00021 X + 1.40	62	0.07	4.28	0.043
Mar	Margin	Y = 0.00024 X + 0.34	20	0.28	7.07	0.016
	Forest	Y = 0.000013 X + 0.33	36	0.04	1.29	0.264
	Grassland	Y = 0.00067 X + 0.38	50	0.47	43.05	<0.001
May	Margin	Y = 0.00021 X + 0.19	24	0.37	12.77	0.002
	Forest	Y = 0.000029 X + 0.20	36	0.11	4.22	0.048
	Grassland	Y = 0.00017 X + 1.50	53	0.08	4.16	0.047
Jul	Margin	Y = 0.00011 X + 0.25	16	0.31	6.17	0.026
	Forest	Y = 0.000005 X + 0.35	31	0.003	0.08	0.783

Figure captions

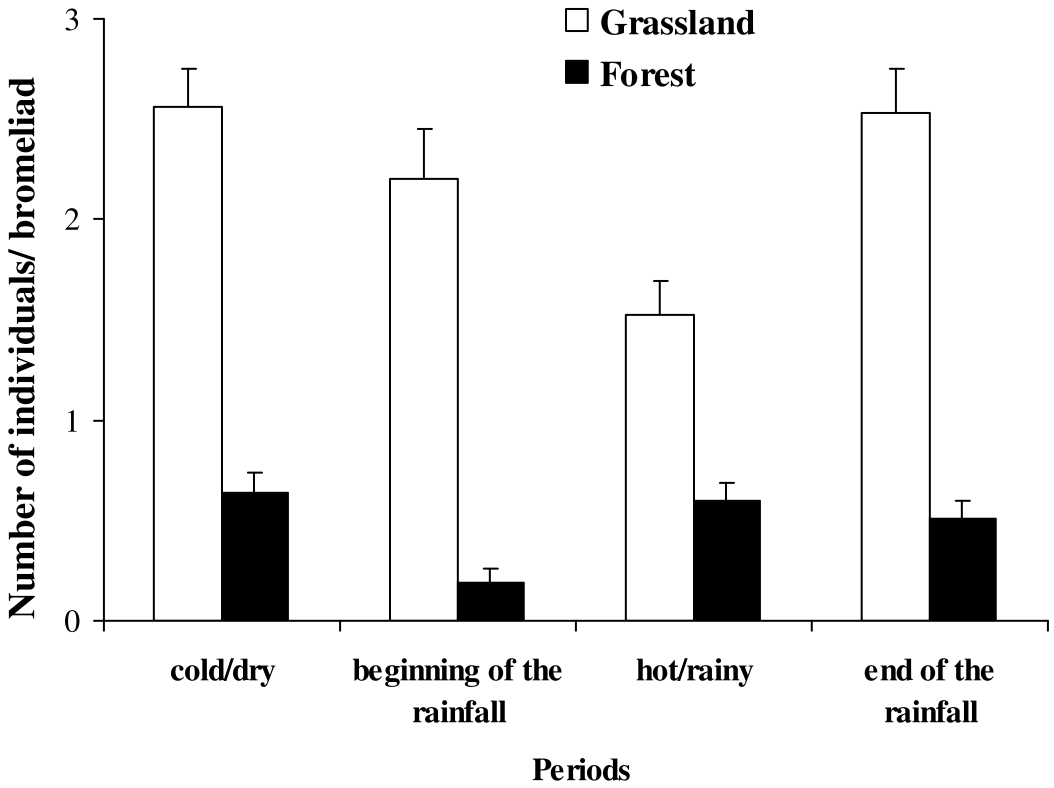
Figures 1--4.–1, Female of *P. chapoda* (arrowhead) under the plain silk cover and on the eggsac produced on a leaf of *B. balansae*; 2, Individual of *B. balansae* in vegetative phenophase in the grassland; 3, in the beginning of inflorescence release (note the central leaves folding back); 3, with presence of infrutescence. (Photos: G.Q. Romero).

Figure 5.–Seasonal variation in the mean density of *Psecas chapoda* individuals on *Bromelia balansae* in grassland (open bars) and in forest (black bars). The sampled periods were: cold/dry = July 98, beginning of the rainfall = October 98, hot/rainy = February 99, end of the rainfall = April 99. Error bars are ± 1 SE.

Figure 6.– Frequency of bromeliads with and without inflorescence occupied by *Psecas chapoda*, in December 1998 and 1999. The values above the bars indicate number of bromeliads examined. G-test with Yates' correction ($G_{1998} = 13.6$, 1 df, $P < 0.001$; $G_{1999} = 15.6$, 1 df, $P < 0.001$).

Figures 7--12.–Distribution of *Psecas chapoda* individuals with different age class (7-11) and of adult females with eggsacs vs. adult + subadult females without eggsacs (12) in the leaf layers of the *Bromelia balansae* rosette (see text for the definitions of layers).

Figures 1-4.



3
2
1
0
Number of individuals/ bromeliad
☐ Grassland
■ Forest
cold/dry
beginning of the rainfall
hot/rainy
end of the rainfall
Periods

Figure 5.

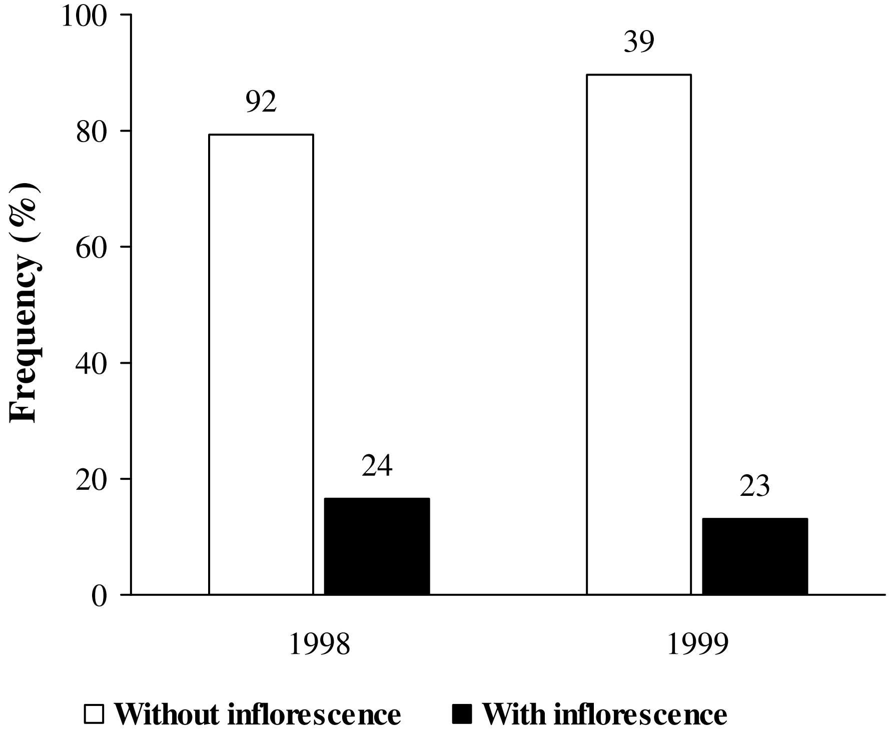
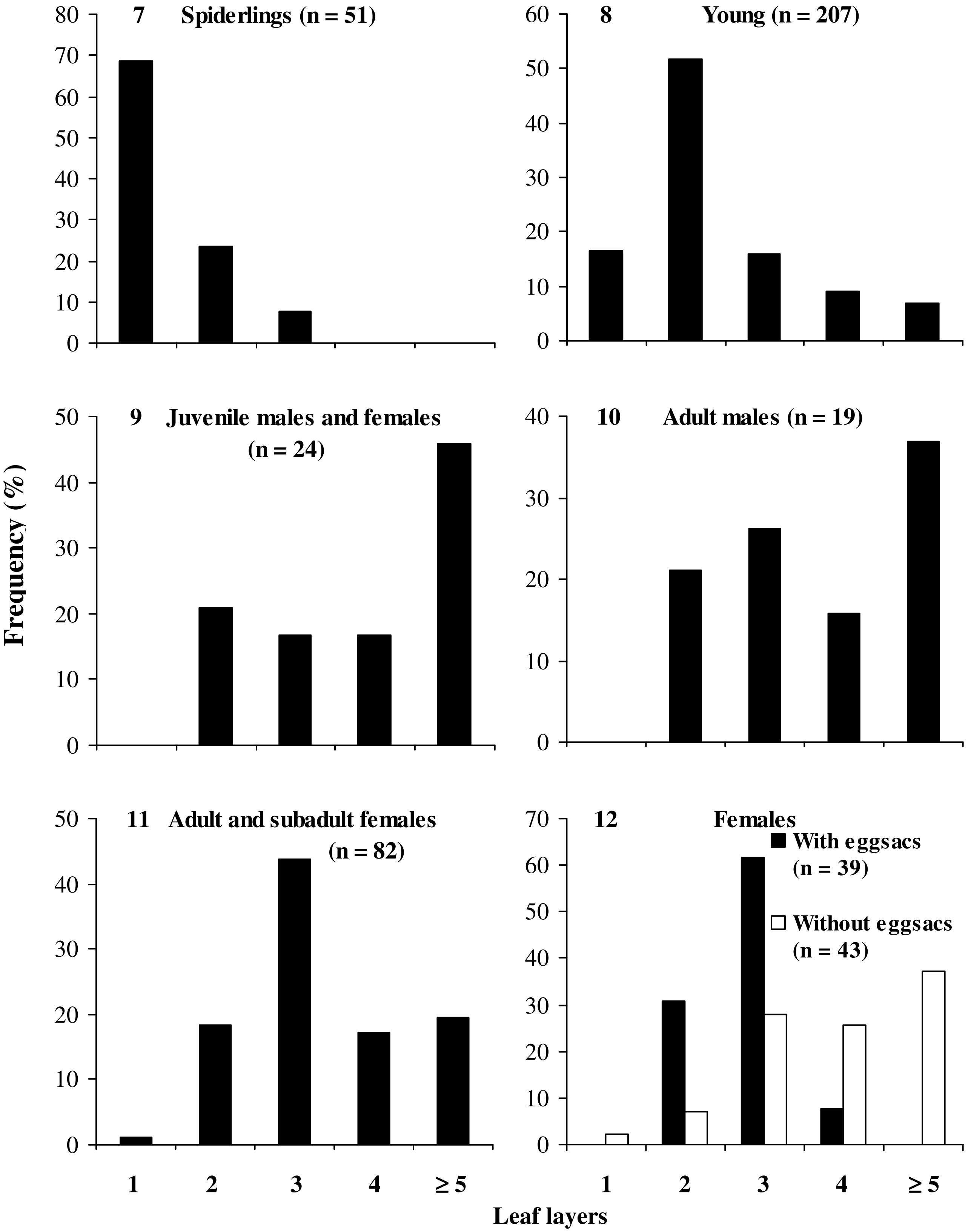

100
80
60
40
20
0
Frequency (%)
92
24
39
23
1998
1999
□ Without inflorescence
■ With inflorescence

Figure 6.

7 Spiderlings (n = 51)
8 Young (n = 207)
9 Juvenile males and females (n = 24)
10 Adult males (n = 19)
11 Adult and subadult females (n = 82)
12 Females
■ With eggsacs (n = 39)
□ Without eggsacs (n = 43)
Frequency (%)
Leaf layers
1
2
3
4
≥ 5
0
10
20
30
40
50
60
70
80

Figures 7-12.

Artigo 4

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

Population dynamics, age structure and sex ratio of the bromeliad-dwelling jumping spider, *Psecas chapoda* (Salticidae)

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In this study, the population fluctuations, phenology and sex ratio of the bromeliad-dwelling jumping spider *Psecas chapoda* were investigated in an area of semideciduous forest in southeastern Brazil. *Psecas chapoda* occurred and reproduced on *Bromelia balansae* (Bromeliaceae) throughout the year. The number of egg sacs increased at the beginning of the rainy season (September-December), but the population size and phenology were stable over time and correlated weakly with rainfall and temperature. The principal factor affecting the dynamics of *P. chapoda* was the blooming of *B. balansae*, which expelled spiders because of the drastic change in plant architecture. Male spiders were more frequent than females during the juvenile phase, whereas females were more frequent than males during the subadult and adult phases, suggesting a sex ratio that favoured males. The biotic and abiotic factors that influence the population dynamics, and sex dependent vulnerability determination are discussed.

KEYWORDS: animal-plant interactions, seasonal fluctuation, age structure, sex ratio, *Psecas*, *Bromelia*, Brazil

Introduction

The phenology of an organism, seen as temporal variations in its life cycle, can be affected by several biotic and abiotic factors. A knowledge of these factors is crucial for understanding a species' population dynamics and community structure (Wolda, 1988). Spiders can adjust their phenology and reproductive periods in response to biotic and abiotic conditions (Reiskind, 1981; Plagens, 1983; Rinaldi and Forti, 1997; Crouch and Lubin, 2000; Rossa-Feres *et al*., 2000; Arango *et al*., 2000, Romero, 2001), to prey availability (Riechert and Luczak, 1982; Riechert and Harp, 1987; Arango *et al*., 2000; Crouch and Lubin, 2000; Romero and Vasconcellos-Neto, in press, a) and the availability of foraging sites (Nentwig, 1993; Arango *et al*., 2000; Romero and Vasconcellos-Neto, in press, b).

The jumping spider *Psecas chapoda* (Peckham & Peckham, 1894), previously identified as *P. viridipurpureus* (Simon, 1901) in Rossa-Feres *et al*. (2000), inhabits *Bromelia balansae* Mez. (Bromeliaceae), a bromeliad that does not accumulate rain water. The entire life cycle, including courtship behaviour, mating, egg laying, and population recruitment of young occur on the bromeliad. Females make up to two egg sacs in the middle region on the concave upper surface of the leaf. These sacs are then covered by a ceiling of silk anchored to the edges of the leaf, with females remaining under this ceiling and above the egg mass (Rossa-Feres *et al*., 2000). During blooming, *B. balansae* folds its leaves to the ground to expose its inflorescence to pollinators. Flowering plants are not occupied by *P.chapoda*, probably because the change in plant architecture does not favour the occupation by the spiders (Romero and Vasconcellos-Neto, unpublished data). Rossa-Feres *et al*. (2000) showed that the phenology of a population of *P. chapoda* occurred in synchrony with the rainy season, in a region with a strongly seasonal climate and a pronounced dry season.

The aims of this study were: 1) to describe the population fluctuations and phenology (seasonal variations in age structure) of *P.chapoda*, 2) to assess whether abiotic factors, such as rainfall and temperature, and biotic factors, such as the blooming periods of *B. balansae* affect the population dynamics of *P. chapoda* and 3) to determine the sex ratio of this spider population.

Material and methods

Study area

This work was done in a grassland area, between a dam and a 1.5 ha fragment of semideciduous forest, close to the city of Dois Córregos (22º 21' S, 48º 22' W), São Paulo state (southeastern Brazil). Only one terrestrial bromeliad species, *Bromelia balansae*, occurs in this region. *B. balansae* is a large bromeliad, with a leaf length reaching 2.5 m in the forest and ~1.2 m in open areas (grasslands). The leaves have large, curved spines spaced 2.5-3.5 cm apart. This perennial bromeliad lives ~ 3-5 years (G. Q. Romero, personal observation), does not accumulate rain water in its rosette and blooming occurs at the beginning of rainfall (Rossa-Feres *et al*., 2000).

Population dynamics of P. chapoda

The population dynamics of *P. chapoda* were assessed between May 1998 and May 2000 by monthly inspections of 23-145 *B. balansae* plants, that were previously marked in grassland (open area), along a 250 m transect 15 m from the forest edge. When young individuals of *B. balansae* appeared, they were also marked. The number of *P. chapoda* individuals and egg sacs was recorded for each plant inspected. Plants that had mature fruits or fruits already dispersed were not inspected since in these phenophases the plants showed traces of senility (wilted or dried leaves) or had already died.

The seasonal fluctuations were determined by the spider density (individual number/bromeliad) over time. The phenology was represented by the temporal variation in spider age structure (e.g. Peck, 1999). To determine the age structure, the spiders were classified as young (spiderlings, instar 3), juveniles (instars 4 and 5), juvenile males and females (instar 6), subadult males and females (instar 7) and adult males and females (instar 8). Each instar and sex of *P. chapoda* had a specific spot and colour pattern (Rossa-Feres *et al*., 2000; G. Q. Romero, personal observation) that facilitated identification of the individuals. However, juvenile, subadult and adult females had the same spot and colour pattern. Juvenile females were small and about the same size as juvenile males (up to 1.1 cm in length), and were easily distinguished from other females. Subadult and adult females were the same size (up to 1.6 cm in length), which made the identification of these age classes difficult. Because of the difficulty in capturing these females to determine their sex, adult and subadult females were grouped for subsequent analysis.

Synchrony and displacement between events

Linear regression analysis (Zar, 1996) was used to assess whether climatic factors (rainfall and temperature) affect the seasonal fluctuations in *P. chapoda* (number of spiders/bromeliad), with up to three months of displacement from the dependent variable. The dependent variable was spider fluctuation and the independent variables were climatic factors, with all variables (dependent and independent) was being obtained monthly. The temperature and rainfall data were obtained from the experimental station at Itauna farm, 5 km from the study area. The data representing densities were normalized by log or log (n + 1) transformations.

Blooming of B. balansae *and the dynamics of* P. chapoda

To verify whether the blooming of *B. balansae* affects the occurrence and population dynamics of *P. chapoda*, 116 and 74 bromeliads were randomly selected in August 1998 and 1999, respectively, and then monitored monthly for flowering and for the number of spiders. These inspections were done up to December of the respective years, since by this time all of the bromeliads had flowered (G.Q. Romero, personal observation). Two groups of bromeliads were thus identified, one which flowered between August and December and one that did not flower until December of 1998 or 1999. The spider densities in these two groups of bromeliads were compared using repeated measures ANOVA (Zar, 1996), in which the months were considered as the repeated factor.

The size (surface area) of the bromeliads belonging to these sets was estimated in August 1998 and 1999 by measuring the length (L) and breadth (B) of a leaf from the middle layer. The product of L x B was multiplied by 0.5 to estimate the leaf area, since the leaf shape resembled an isosceles triangle. The resulting area was multiplied by the total number of green leaves of the bromeliad to estimate the surface area of the plant.

Sex ratio

The sex ratio of *P. chapoda* was monitored monthly throughout the study and was calculated for juvenile males vs. females (antipenultimate instar) and for adult + subadult males vs. adult + subadult females. Adult and subadult instars were grouped because of difficulties in determining the age of adult and subadult females. The sex ratios of each instar in each month were compared using the G-test (Zar, 1996).

Voucher specimens of *P. chapoda* were deposited at the "Coleção Aracnológica do Laboratório de Artrópodes Peçonhentos do Instituto Butantan" under the accession number IBSP 16242.

Results

Population dynamics, synchrony and displacement between events

Psecas chapoda occurred on *B. balansae* throughout the year during the two years of observation (figures 1 and 2), and also produced egg sacs throughout the year (figure 1). The size of the *P. chapoda* population varied little over time (figure 1). However, the mean number of individuals per bromeliad (spider density) varied between the months of 1998 (ANOVA; $F_{7,629} = 4.53$; $P < 0.001$) and 1999 (ANOVA; $F_{11,843} = 6.35$; $P < 0.001$), and was lower in August and September in 1998, and in February and March, and from August to

October in 1999 (figure 2). The number of egg sacs varied seasonally and was higher in May and from August to December in 1998 and from September to December in 1999 (figure 1), the latter two periods corresponding to the beginning of rainfall (figure 3). Like the spiders, the bromeliads also reproduced at the beginning of rainfall (figures 1 and 3).

The *P. chapoda* density correlated positively, but slightly, with rainfall 1-2 months after the beginning of rainfall, but correlated positively with temperature only after three months of increased temperature (table 1, figures 1-3). The females produced more egg sacs 2-3 months after the beginning of rainfall and increased temperature (table 1, figures 1 and 3). *Bromelia balansae* flowered from September to December, one month after the beginning of rainfall ($r^2 = 0.29$; $P = 0.008$; figures 1 and 3).

The phenogram (figure 4) shows that the age structure of *P. chapoda* varied little during the two years of the study. Although instars occurred in all seasons because the females produced egg sacs throughout the year, there was an increase in spiderling frequency in September (figure 4) at the beginning of the rain season (figure 3). In 1998, the number of spiderlings peaked in October and continued elevated until April 1999. In September and December 1999, the frequency of spiderlings was high, but with no well-defined peak. In contrast, the other age classes were structurally very stable over time (figure 4).

Blooming of B. balansae *and the dynamics of* P. chapoda

In the period that preceded the reproduction of *B. balansae* (August), the group of plants that had not yet flowered between August and December had a higher number of spiders compared to those that did not flower until December. This phenomenon was observed in 1998 ($F_{1,101} = 25.40$; $P < 0.001$; figure 5 A) and 1999 ($F_{1,70} = 4.93$; $P = 0.030$; figure 5 B). The size of plants ready to reproduce was greater than those not ready to reproduce in 1998 (mean ± SE in cm^2; to reproduce: 8595.34 ± 1084.78; others: 3418.13 ± 442.84; Mann-Whitney U test; T = 1860; P < 0.001) and 1999 (to reproduce: 6269.05 ± 817.22; others: 3791.64 ± 400.61; Mann-Whitney U test; T = 931, P = 0.002). The population size of *P. chapoda* seems not to be affected by *B. balansae* blooming (figure 1). However, the number of spiders in the group of bromeliads that flowered decreased as the proportion of these bromeliads increased (figures 5 A and B). In contrast, the number of spiders in the group of plants that did not flower until December increased (figures 5 A and B). The interactive effect of the bromeliad groups (with vs. without inflorescence) and time was significant in both years (table 2).

Sex ratio

Throughout the year, adult and subadult females were more frequent relative to males of the same age. In contrast, juvenile males belonging to the antipenultimate instar were more frequent compared to females of the same age (table 3).

Discussion

Psecas chapoda inhabited *B. balansae* throughout the year, suggesting a strong association of the spider with this plant. In addition, males were frequently seen displaying courtship behaviour throughout the year (G. Q. Romero, personal observation) and females also produced egg sacs in all months, thus reinforcing the hypothesis of a high level of spider-plant association. Females generally tend to maximize their offspring survivorship by choosing suitable, safe sites to oviposit (Morse, 1990, 1992, 1993; Harvey, 1994). *Bromelia balansae* must be an excellent site for reproduction and spiderling survival, since its leaves have a large surface area that facilitates the courtship behaviour of males, and the rosette of this plant has microhabitats and small spaces that shelter spiderlings against desiccation and predation. The leaves also have large spines that can protect adult and immature spiders against vertebrate predators.

The high stability of the seasonal fluctuations and age structure over time indicated that there was generation overlap in this population of *P. chapoda*. In contrast, Rossa-Feres *et al*., (2000) reported that another population of *P. chapoda* studied 200 km from our site showed strong population recruitment characterized by the sequential appearance of spiderlings, juveniles, subadults and adults throughout the seasons. These authors also reported that mating in this population of *P. chapoda* occurred only between August and March, with egg sacs appearing only from November to March, and in July. Rain was suggested to be influential in moulding the phenological patterns of the population since the climate was strongly seasonal (Rossa-Feres *et al*., 2000). However, the climate at our site was also strongly seasonal (figure 3). The proximity of the bromeliads to the dam could have provided this spider population with allochthonous resources. Throughout the year, dipterans of the family Chironomidae emerge from this dam and are captured by the spiders (G.Q. Romero, personal observations). This additional food source has probably helped to maintain the dynamics of this spider population stable. Polis and Hurd (1995) showed that the density of spiders on some plant species was low when distant from the sea coast, but high when close to sea level, because the high density of detritivorous insects (allochthonous input) coming from organic matter deposited by the sea enhanced the carrying capacity of the spider population.

In contrast to the low variation in the number of individuals, the number of egg sacs increased 2-3 months after the beginning of the rain. This finding was similar to that of Rossa-Feres *et al*. (2000). Rain was probably a stimulus for adult spiders to begin mating and laying eggs.

The blooming of *B. balansae* clearly affected the density of *P. chapoda* because the altered architecture of the plant with the folding of its leaves to the ground, expelled the spiders (G.Q. Romero and J. Vasconcellos-Neto, unpublished data). However, this effect must be cryptic in the population since the spider population fluctuated very little. This limited fluctuation probably reflected the fact that the frequency of bromeliads in bloom in the population was not very high (21-37%), and that the spiders may have migrated to neighbouring bromeliads when expelled by the blooming bromeliad. The large variation in the density of spiders per bromeliad and the increasing number of spiders on plants that lacked inflorescence could reflect this migration of *P. chapoda* from plants with inflorescence to those without. These results suggest that the blooming of *B. balansae* can influence the size and growth of the *P. chapoda* population and, the spider population dynamics. Theoretically, if all of the bromeliads of the population bloomed at the same period, the spider population could be driven to local extinction. This system thus provides good conditions for studying population dynamics in metapopulations (see Hanski and Gilpin, 1991).

Whereas females were more frequent in the adult and subadult phases compared to males, in the antipenultimate instar (juvenile males and females), the frequency of males was higher than females, suggesting that this *P. chapoda* population has a sex ratio skewed towards males. During courtship display, the males always maintain a higher position on the leaf, while the female is lower down, close to the bromeliad base, where it is protected against predators. In this courtship behaviour, the males move a lot and can easily be detected by a predator (Rossa-Feres *et al*., 2000). Moreover, males must spend more energy on courtship, and hence they probably die faster than females. Males also move among bromeliads more often than females (G. Q. Romero, personal observations), with the latter remaining for a long time below the ceiling of silk built to protect themselves and the egg sacs (Rossa-Feres *et al*., 2000). In their migrations out of the plant, the males become more vulnerable to attack by natural enemies. Hence, natural selection may have skewed the sex ratio to males since the rate of mortality among males must be higher than for females, as also occurs in several other organisms (see Halliday, 1994).

In conclusion, *P. chapoda* was strongly associated with *B. balansae* since the spider inhabited and reproduced on the plant throughout the year. Abiotic factors (e.g. rainfall) appear to stimulate mating and the laying of eggs, but do not affect the spider population dynamics. However, the blooming of *B. balansae* results in a dramatic change in plant architecture that expels *P. chapoda* and affects the spider population dynamics. More males than females are born in this population, possibly because the mortality rate of males is higher than for females. This higher mortality may reflect the greater energy spent in courtship behaviour and the vulnerability of males to predation.

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Table 1. Regression analysis examining the effects of rainfall and temperature on the density of *Psecas chapoda*, displaced one, two and three months relative to the dependent variable (spider density).

	Displacement (in months)	r^2	*F*	*P*
Rainfall vs. no. of spiders				
	0	0.01	0.23	0.630
	1	0.17	4.31	0.050
	2	0.18	4.36	0.050
	3	0.07	1.51	0.230
Temperature vs. no. of spiders				
	0	0.06	1.45	0.242
	1	0.10	2.43	0.134
	2	0.16	3.75	0.067
	3	0.36	10.77	0.004
Rainfall vs. no. of egg sacs				
	0	0.01	0.28	0.602
	1	0.09	2.09	0.163
	2	0.19	4.70	0.042
	3	0.53	21.86	<0.001
Temperature vs. no. of egg sacs				
	0	0.07	1.73	0.202
	1	0.01	0.15	0.702
	2	0.23	5.73	0.027
	3	0.57	23.98	<0.001

Table 2. Repeated measures ANOVA examining the variation in the density of *Psecas chapoda* on *Bromelia balansae* that bloomed vs. those that did not bloom (bromeliad groups). Time was treated as the repeated factor. The probabilities were corrected against sphericity using the Greenhouse-Geisser (G-G).

Source of variation	df	*MS*	*F*	*P*	*G-G*
1998					
Bromeliad groups	1	19.42	2.14	0.147	
Error	100	9.08			
Time	4	9.32	2.78	0.027	0.046
Bromeliad groups x Time	4	66.29	19.78	<0.001	<0.001
Error	400	3.35			
1999					
Bromeliad groups	1	4.04	0.75	0.389	
Error	58	5.36			
Time	4	19.39	5.44	<0.001	0.002
Bromeliad groups x Time	4	24.49	6.87	<0.001	<0.001
Error	232	3.56			

Table 3. Sex ratios of adult + subadult males and females (Ad + Subad, ultimate and penultimate instars) and of juvenile males and females (antepenultimate instar) of *Psecas chapoda*, between May 1998 and April 2000. The G-tests were calculated using Yate's correction

Months	Individuals	Males (n)	Females (n)	Sex ratio (M : F)	G-test	P
Jan	Ad + Subad	12	64	1 : 5.33	37.41	<0.001
	Juveniles	20	0	1 : 0.00	-	-
Feb	Ad + Subad	17	39	1 : 2.29	4.04	0.044
	Juveniles	15	7	1 : 0.47	2.25	0.134
Mar	Ad + Subad	18	52	1 : 2.89	8.09	0.004
	Juveniles	20	5	1 : 0.25	8.31	0.004
Apr	Ad + Subad	27	57	1 : 2.11	10.23	0.001
	Juveniles	16	11	1 : 0.69	0.59	0.442
May	Ad + Subad	38	59	1 : 1.55	4.15	0.041
	Juveniles	14	12	1 : 0.86	0.04	0.841
Jun	Ad + Subad	41	67	1 : 1.63	5.89	0.015
	Juveniles	23	10	1 : 0.43	4.47	0.034
Jul	Ad + Subad	74	120	1 : 1.62	10.54	0.001
	Juveniles	52	9	1 : 0.17	31.80	<0.001
Aug	Ad + Subad	35	85	1 : 2.43	20.60	<0.001
	Juveniles	34	11	1 : 0.32	11.22	<0.001
Sep	Ad + Subad	51	71	1 : 1.39	2.97	0.084
	Juveniles	17	11	1 : 0.65	0.89	0.345
Oct	Ad + Subad	32	60	1 : 1.87	8.04	0.004
	Juveniles	14	5	1 : 0.36	2.93	0.086
Nov	Ad + Subad	31	60	1 : 1.93	8.76	0.003
	Juveniles	9	10	1 : 1.11	0.00	-
Dec	Ad + Subad	22	50	1 : 2.27	10.39	0.001
	Juveniles	23	8	1 : 0.34	6.55	0.010

Figures Legends

Fig. 1. Fluctuations in the number of *Psecas chapoda* and egg sacs (log) on bromeliads with and without inflorescence, and the frequency (%) of bromeliads in bloom (with inflorescence or infrutescence) between May 1998 and April 2000 (n = 3516 spiders and 314 egg sacs).

Fig. 2. Mean number (± 1 SE) of *Psecas chapoda* per *Bromelia balansae* with no inflorescence, from May 1998 to April 2000 (n = 3516 spiders).

Fig. 3. Climatic data from Itauna farm (5 km from the study site), from May 1998 to April 2000.

Fig. 4. Phenogram of the *Psecas chapoda* population on plants of *Bromelia balansae* without inflorescence, from May 1998 to April 2000 (n = 3516 spiders).

Fig. 5. Mean number (± 1 SE) of spiders *Psecas chapoda* on bromeliads that produced inflorescence between August and December and on bromeliads that did not produce inflorescence until December, in 1998 (A) and 1999 (B). The frequency (%) of bromeliads that bloomed up to December is also shown.

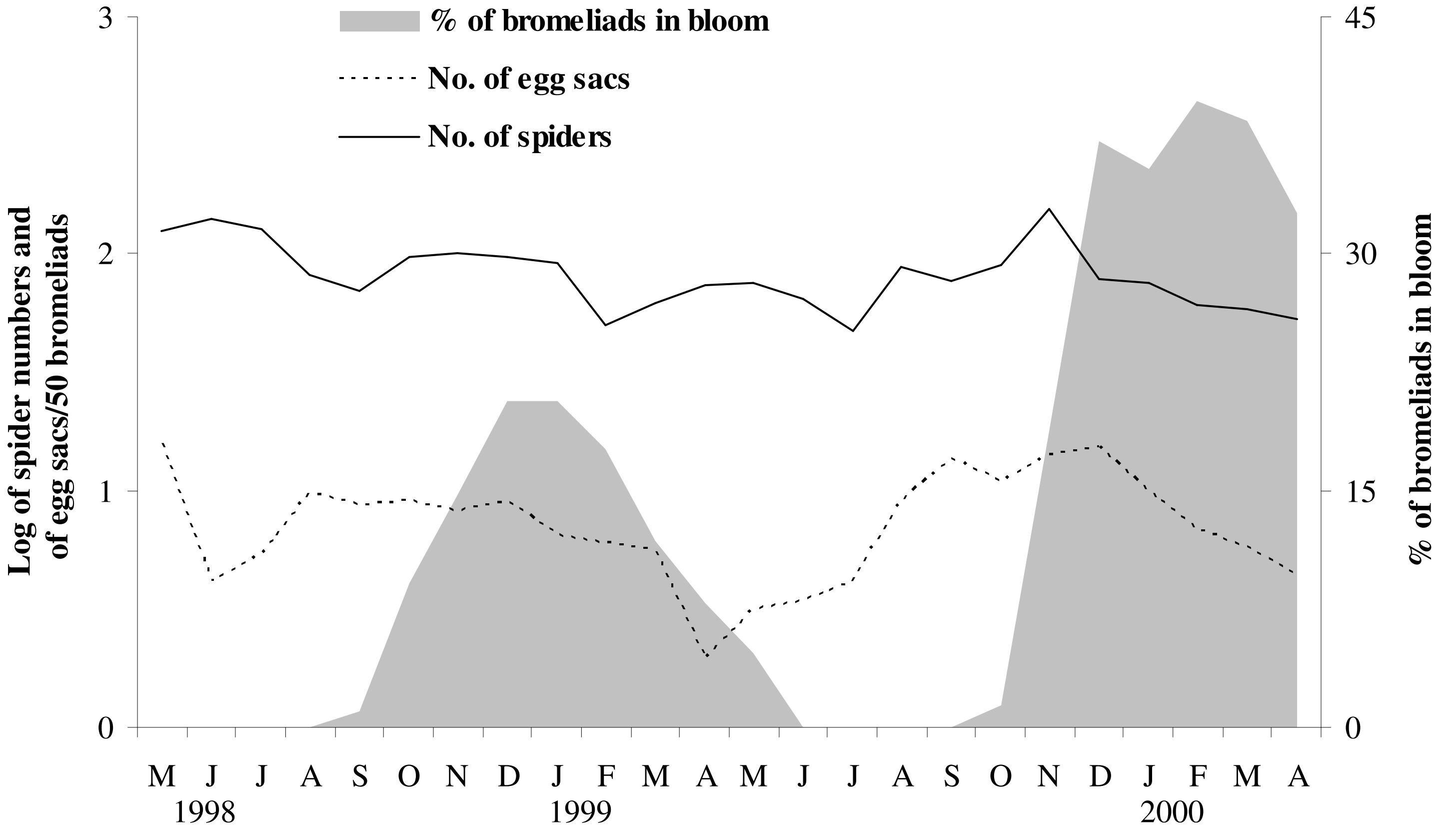

% of bromeliads in bloom
No. of egg sacs
No. of spiders
Log of spider numbers and of egg sacs/50 bromeliads
% of bromeliads in bloom
3
2
1
0
45
30
15
0
M J J A S O N D J F M A M J J A S O N D J F M A
1998
1999
2000

Fig. 1.

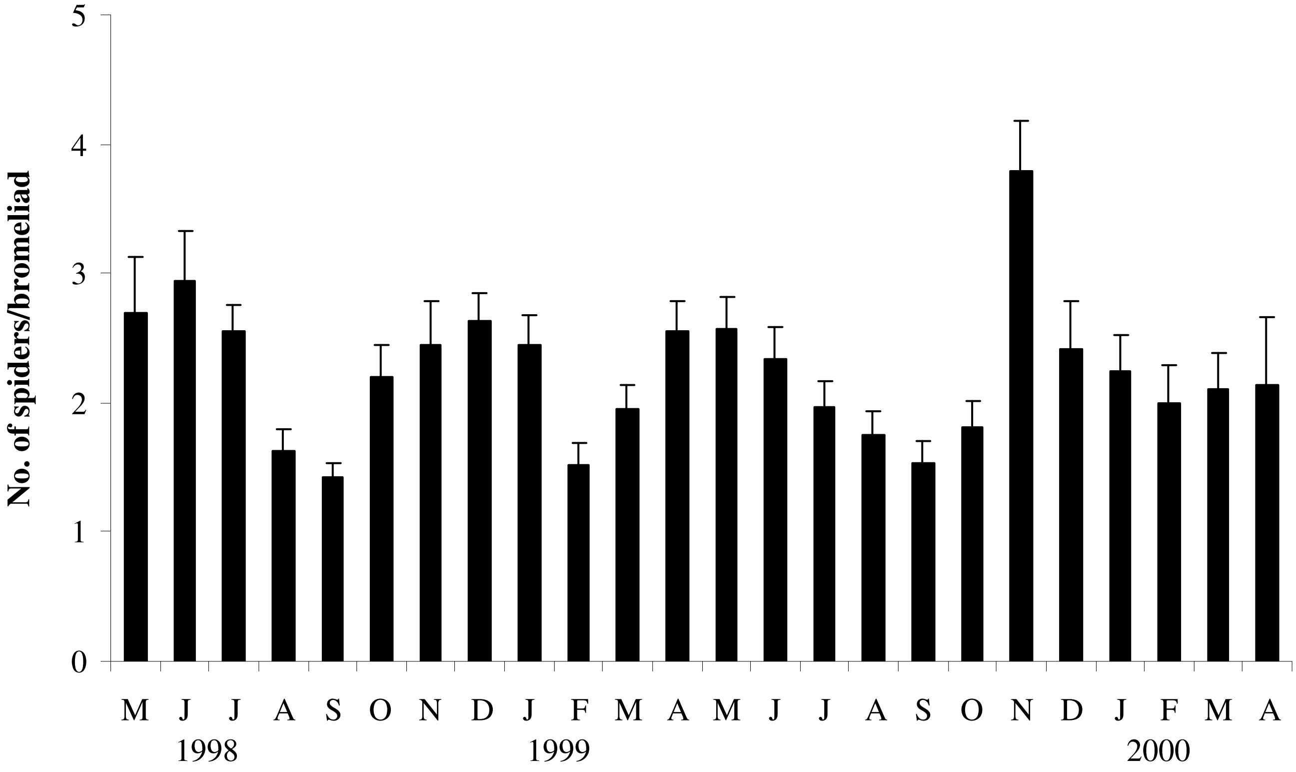
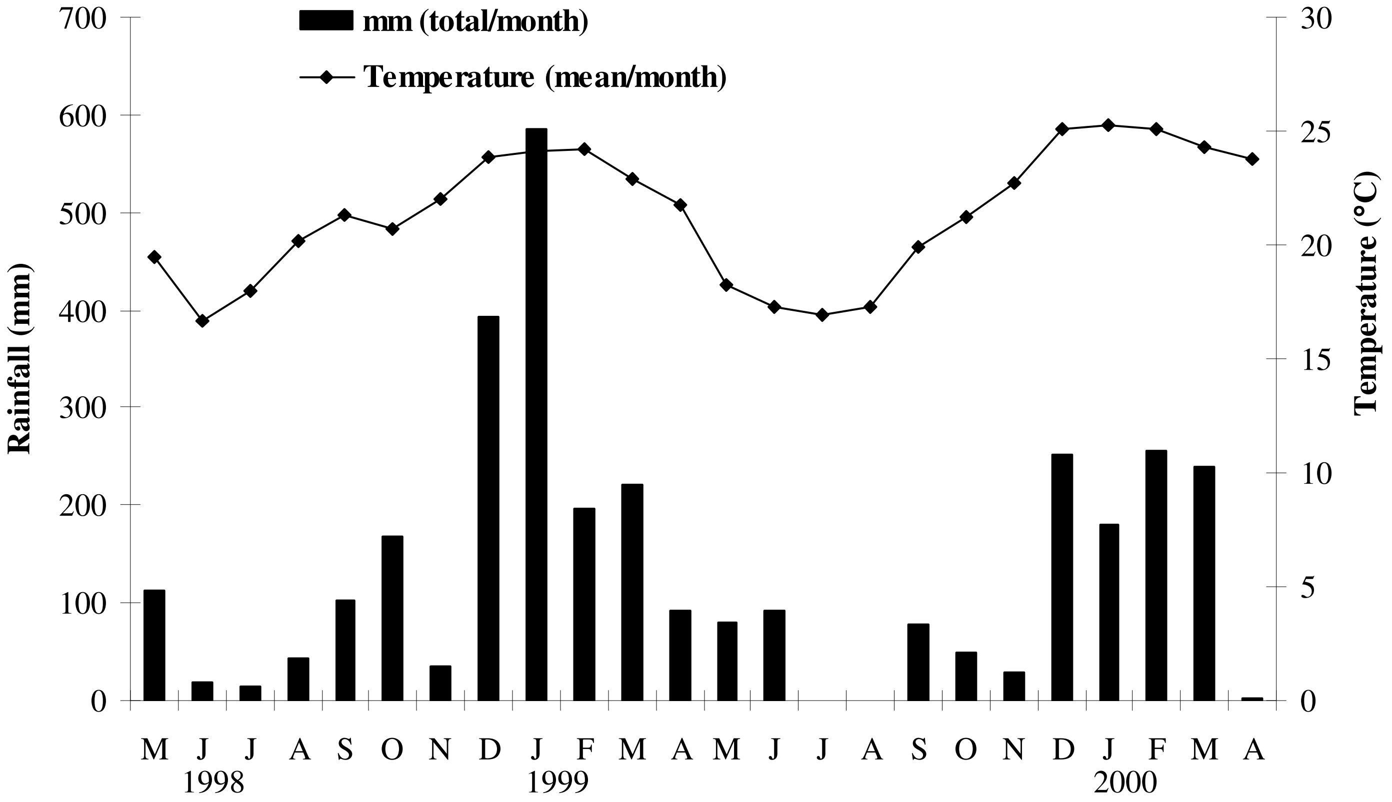

No. of spiders/bromeliad
0
1
2
3
4
5
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
1998
1999
2000

Fig. 2



mm (total/month)
Temperature (mean/month)
Rainfall (mm)
Temperature (°C)
0
100
200
300
400
500
600
700
0
5
10
15
20
25
30
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
1998
1999
2000

Fig. 3.

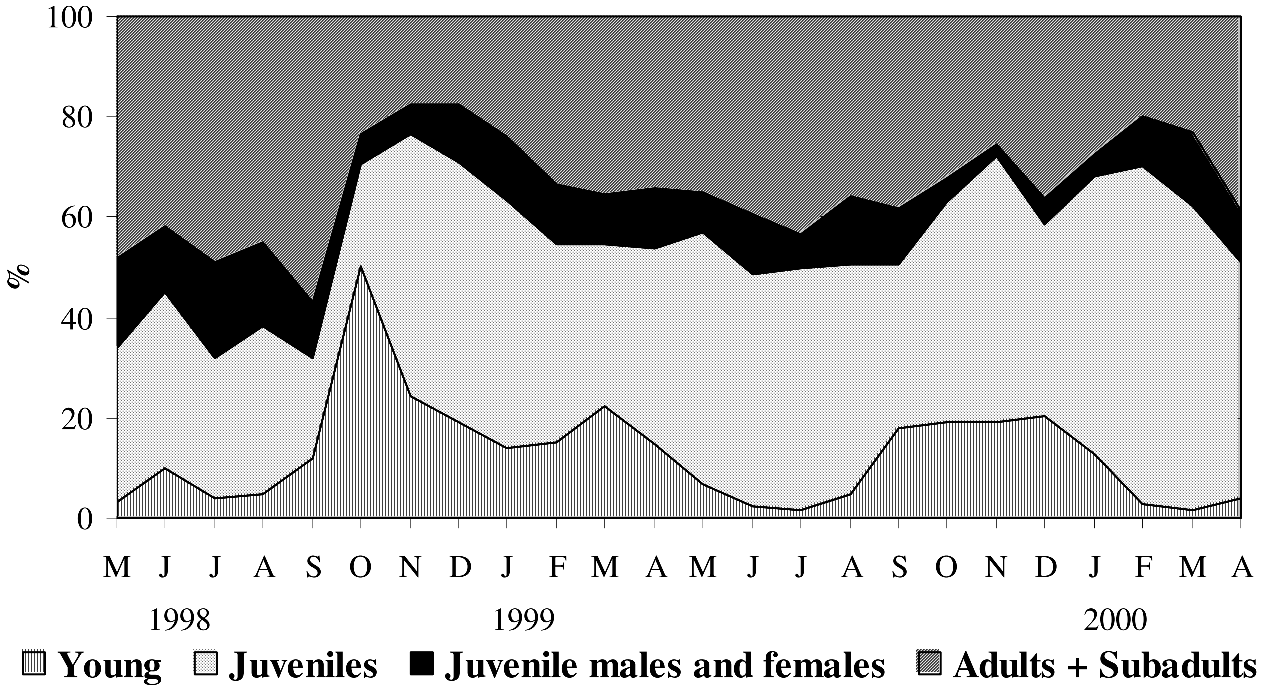

100
80
60
40
20
0
%
M J J A S O N D J F M A M J J A S O N D J F M A
1998
1999
2000
Young
Juveniles
Juvenile males and females
Adults + Subadults

Fig. 4.

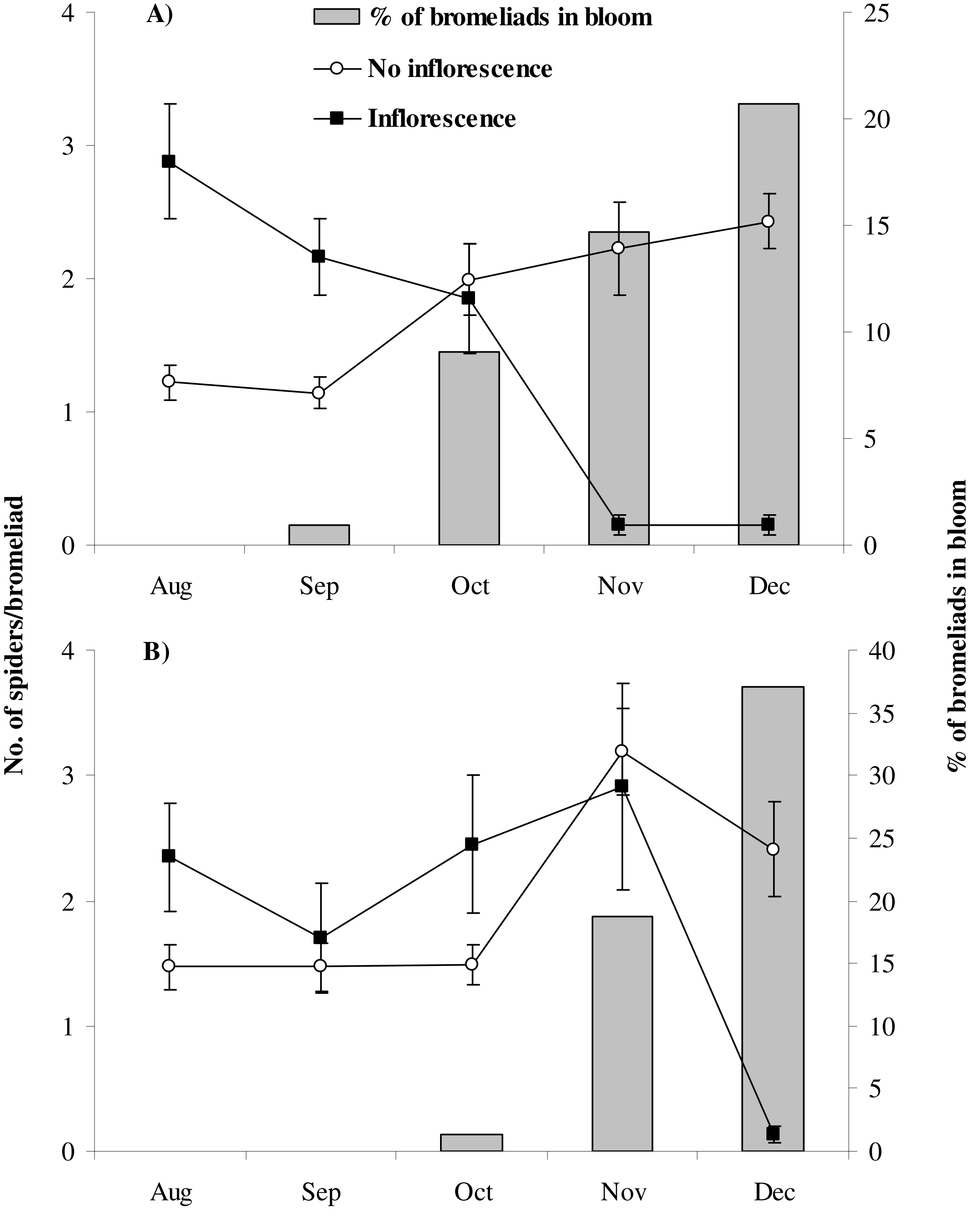

A)
% of bromeliads in bloom
No inflorescence
Inflorescence
B)
No. of spiders/bromeliad
% of bromeliads in bloom
0
1
2
3
4
0
5
10
15
20
25
30
35
40
Aug
Sep
Oct
Nov
Dec

Fig. 5.

Artigo 5

Romero, G.Q. & Vasconcellos-Neto, J. 2005. 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.

The effects of plant structure on the spatial and microspatial distribution of a bromeliad-living jumping spider (Salticidae)

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Running title: Plant structure affect spider distribution

Summary

1. In several regions of South America, the neotropical jumping spider *Psecas chapoda* inhabits and reproduces strictly on the bromeliad *Bromelia balansae*. Previous studies reported that this spider is more frequent on bromeliads in grasslands than on those growing in forests, and on larger plants, but only when the bromeliads are without inflorescence. Upon blooming, *B. balansae* fold their leaves back, thereby changing the plant architecture from a tridimensional to a bidimensional flattened shape, and our hypothesis is that this alteration affects the spider's habitat-selection decisions.

2. In the present study, we examined experimentally the effects of inflorescence, plant size, and blockade of the axil of the leaves (spider shelters) of forest bromeliads on the colonisation of a bromeliad by *P. chapoda*. By using sticky traps, we also compared prey availability in grassland and forest.

3. Plants with simulated inflorescence were colonised at a lower frequency than those without inflorescence simulation. Grassland bromeliads in which the rosettes were blocked with dry leaves were colonised less frequently than open bromeliads, whereas forest bromeliads from which dry leaves had been removed were not colonised. Spiders generally abandoned bromeliads in which three-quarters of the length of the leaves had been removed, although females with eggsacs remained on these plants. Prey availability (biomass and number) was up to 18 fold higher in the grassland than in the forest. These results suggest that microhabitat structure and prey availability shape the spatial distribution of *P. chapoda* populations.

4. Our findings suggest that *Psecas chapoda* can evaluate, in fine detail, the physical state of its microhabitat, and this unusual spider-plant association is readily destabilised by changes in the microhabitat (i.e., it is strictly dependent of the size and morphology of the host plant). This study is one of the few to report a strict association between a spider species and its host plant, and also one of the few to examine the effects of habitat and microhabitat structure on the spatial distribution of active hunters on plants.

Key-words: animal-plant interaction, bromeliad architecture, habitat and microhabitat structure, *Psecas chapoda*, Salticidae, spider colonisation

Introduction

Structural components of the vegetation exert a strong influence on the density and diversity of many terrestrial arthropods (Lawton 1983; Morse *et al*. 1985; Scheuring 1991; Gunnarsson 1992; Gardner *et al*. 1995; Borges & Brown 2001), but spiders appear to be particularly strongly influenced by architectural variations in the vegetation (Riechert & Gillespie 1986; Gunnarsson 1996). Spiders do not eat plants, but plants are often important for them as sites for building webs (Lubin 1978; Rypstra 1983; Greenstone 1984; Herberstein 1997; Figueira & Vasconcellos-Neto 1991), for sheltering against desiccation (Riechert & Tracy 1975) or natural enemies (Gunnarsson 1990, 1996), for foraging (Morse & Fritz 1982; Morse 1990; Scheidler 1990; Schmalhofer 2001; Romero & Vasconcellos-Neto 2003, 2004a,b), and for mating and oviposition (Rossa-Feres *et al*. 2000; Smith 2000; Romero & Vasconcellos-Neto 2003, in press, a, b). That plant architecture affects the abundance and distribution of spiders has been shown for a variety of spiders (Colebourne 1974; Greenquist & Rovner 1976; Robinson 1981; Rypstra 1983; Gunnarsson 1990, 1992), and thomisid spiders have been shown actively to select plant-determined microhabitat (Morse & Fritz 1982; Morse 1990, 1993).

Even when there is an apparent relationship between changes in plant architecture and spider density, whether the causal relationship is direct or indirect is often uncertain because potentially important environmental factors, such as prey availability (Rypstra 1983; Greenstone 1984; Halaj, Ross & Moldenke 1998) can vary with the habitat structure. Any strong conclusions about plant architecture directly affecting spider distribution require experimental support (Wise 1993). For example, experiments based on artificial vegetation or direct manipulation of the structures of live plants have shown that spiders from different taxonomic groups and from different guilds have specific preferences for certain types of architecture (Robinson 1981). Other experimental studies have shown that the reduction in the number of foraging or shelter sites, and changes in the substrate abundance, negatively affected the density of particular spider species (Gunnarsson 1990; McNett & Rypstra 2000). However, all previous experimental studies have examined how the density web-building spiders is influenced by habitat structure. There have been no experimental studies on how plant architecture might influence density of hunting spiders.

The spider *Psecas chapoda* (Peckham & Peckham) (Salticidae) inhabits and reproduces strictly on *Bromelia balansae* Mez. (Bromeliaceae) (Rossa-Feres *et al*. 2000; Romero & Vasconcellos-Neto, in press, a, b) in several regions of Brazil, Paraguay, and Bolivia (Höfer & Brescovit 1994; Rossa-Feres *et al*. 2000; Romero & Vasconcellos-Neto, in press, a, b; G.Q. Romero, unpublished data). This spider occurs at a higher density on *B. balansae* in grassland (open areas) than on bromeliads growing in forest. Romero & Vasconcellos-Neto (in press, a) suggested that dry leaves falling from trees in the forest negatively affected the colonisation of these bromeliads by blocking the base of bromeliad rosettes used as shelter by the spiders. Spider density was also lower in plants with inflorescence (or infrutescence), possibly because of the changes in plant architecture during blooming (Romero & Vasconcellos-Neto, in press, a, b). Romero & Vasconcellos-Neto (in press, a) found a positive relationship between length of bromeliad leaves and number of spiders on the plants, and suggested that the carrying capacity is positively related to bromeliad size.

Here we use this spider-plant system for investigating the effects of changes in microhabitat architecture on spider density. We consider the spider's selection of microhabitats for shelter, foraging, mating, and oviposition. In our experiments, we examine how colonisation and selection of microhabitats by *P. chapoda* is influenced by plant size, inflorescence and accessibility to rosettes of *B. balansae*. Specifically, we addressed three questions. 1) How many spiders colonise plants without inflorescence and without dry leaves in their rosette compared to how many colonise plants with inflorescence and dry leaves? 2) Does spider age influence colonisation pattern? 3) Do leaf size affect density of spiders on bromeliads? We also consider whether prey availability in forest and grassland differ.

Material and methods

STUDY AREA AND ORGANISMS

This work was carried out from October 2001 to February 2003 in a 250 m x 60 m fragment of semideciduous forest and in an adjacent grassland area along the margin of a river. This site was near Dois Córregos city (22º 21' S, 48º 22' W), São Paulo state, in southeastern Brazil. Local climate consists of a distinct dry/cold (May-September) and wet/warm (October-April) season. Mean annual rainfall is 1600 mm (Romero & Vasconcellos-Neto, in press, b).

The entire life cycle of *P. chapoda*, including courtship behaviour, mating, oviposition, and spiderling recruitment occurs on the bromeliad *B. balansae*. Females lay 1-3 eggsacs on the concave side of the central region of the leaves. The eggsacs are wrapped in a plain silk cover (nest) that is spun at the edge of each leaf, and the females remain under the nest (Rossa-Feres *et al*. 2000). When we attempted to capture the spiders, they tended to run to the rosette base (G.Q. Romero, pers. obs.). This suggested that the bromeliad was especially suitable as shelter against predation. In the study area, *B. balansae* was present in grassland and forest at comparable density (Romero & Vasconcellos-Neto, in press, a). These bromeliads do not accumulate rain water. They bloom at the beginning of the rainy season (September-December), and up to 40% of the individuals release the inflorescence (Romero & Vasconcellos-Neto, in press, b).

EXPERIMENT 1: SIMULATION OF THE INFLORESCENCE

The objective in this experiment was to investigate whether the presence of inflorescence influenced the spider's inclination to take up residence in plants (bromeliad affinity). Different age classes of spiders were tested for evidence of whether bromeliad affinity changes during the life cycle. For this, 52 individuals of *B. balansae* were brought from other sites and planted in pairs (blocks) in the grassland of the study area. The bromeliads used were all of similar size (median leaf length ~50-70 cm). A distance of 2 m separated plants of the same pair, and each pair was at least 4-6 m from its nearest neighbour. One bromeliad in each pair was randomly chosen for inflorescence simulation (experimental) while the other bromeliad was unaltered (control). To simulate inflorescence, an iron ring (16 cm in diameter) was placed on top of the central region of the rosette and then pressed down to force the leaves of the external and internal layers to the ground, where they remained parallel with each other and with the soil. The rings were kept in this position by three iron supports that were fixed perpendicular to each ring and anchored in the soil. The rings and supports were 5 mm in diameter. Only the leaves of the first one or two layers of the experimental plants were not bent by the ring. This was because of their small size. However, all other leaves were altered. In the control plants, the ring was positioned normally, but was not pressed down (i.e., plant architecture was not altered). There was no evidence that the rings changed the behaviour or abundance of spiders on the control plants.

Before the experiment began, all plants were inspected to ensure that they had not already been colonised by *P. chapoda* (individuals and eggsacs). The spiders and eggsacs on each plant were censused fortnightly after the beginning of the experiment (October 5, 2001). Only new eggsacs (with plain silk cover, see Rossa-Feres *et al*. 2000) were censused in these samples. Age-specific patterns of spots and coloration were used to identify *P. chapoda* as spiderlings (3rd instar), young (4th and 5th instars), juvenile males (up to 1.1 cm in body length), juvenile females (6th instar), subadult male (7th instar) and adult males (8th instar) (Romero & Vasconcellos-Neto, in press, a). Although sex-specific patterns of spots and coloration are useful for discriminating subadult and adult stages, subadult and adult females have the same spot and coloration patterns, and a similar size (up to 16 mm in body length), making it difficult to determine their instar in the field (Romero & Vasconcellos-Neto, in press, a). Since the capture of these spiders on the bromeliads was very difficult, we included subadult and adult females (7th and 8th instars) in the same class for analysis.

EXPERIMENT 2: ADDITION/REMOTION OF DRY LEAVES

The hypothesis here is that dry leaves falling from forest trees block the base of *B. balansae* rosettes (the shelter used by the spiders) and make them difficult for the spider to access. Dry leaves on the bromeliads, therefore, could be changing the patterns of spider distribution between habitats (grassland/forest). To test this hypothesis, 36 bromeliads of a similar size were brought from other sites and freed of spiders and eggsacs before planting in pairs (blocks) in the grassland of the study area, as in experiment 1. Both plants of each pair initially received dry leaves brought from the rosettes of forest bromeliads. However, for one individual chosen at random in each pair, all of the dry leaves were removed (control). In the forest area, dry leaves were removed from the interior of 10 bromeliads of similar size (experimental), 10-20 m apart from the grassland, while the 10 bromeliads of similar size closest to the experimental plants (within 0.5-1.5 m) were left with their natural accumulation of dry leaves (control). These forest bromeliads had no spiders or eggsacs. The spiders and eggsacs were censused once every 10-15 days after the start of the experiment (September 20, 2002).

EXPERIMENT 3: CUTTING OF BROMELIAD LEAVES

Psecas chapoda uses *B. balansae* leaves as foraging sites, and a shortening of the leaves might decrease spider density by the decreasing the carrying capacity of the microhabitat. Something similar has been reported in other studies on other spiders (Gunnarsson 1990). To test this hypothesis, 30 individuals of *B. balansae* of similar size (see experiment 1) in the natural population from grassland were selected along a 250 m transect and numbered. In the first plant found, three-quarters (¾) of the total length of all of the leaves was removed (treatment 1), in the second plant, one-quarter (¼) of the total length of all of the leaves was removed (treatment 2), and in the third plant no leaves were cut (control). This sequence of treatments was repeated until 30 plants had been included (10 plants/treatment). In the control plants, the leaves were slightly shaken to simulate the leaf cutting in the other treatments. The number of spiders and their eggsacs on each plant was censused before the start of the experiment (December 30, 2002), and after 1, 2, 3, 4, 5 and 19 days.

PREY AVAILABILITY

Even if rosettes blockage by dry leaves affects spider distribution, another influence might be prey availability. We consider this hypothesis by determining how prey number and prey biomass varied between forest and grassland. For this, we used 10 sticky-traps set up 40-60 cm above the ground at 10 m intervals in the vegetation amongst the bromeliads. These traps were put in place on two parallel transects (10-30 m apart), one in grassland and the other in forest, on November 9 and 23 (2002), January 18 (2003) and February 12 (2003). Each of these were sunny days with little or no wind. The traps remained in place between 9:00 a.m. and 6:00 p.m., which corresponded to the period of highest foraging activity of *P. chapoda* (G. Q. Romero, pers. obs.). Each trap consisted of a wooden frame (20 cm x 15 cm) covered with commercial transparent plastic (DAC Ltd.), as well as resin Tanglefoot (Tanglefoot Co., Grand Rapids, MI) on one of its surfaces. This trap type was used because it captures flying insects that randomly colonise bromeliads, these being the insects that comprise the main part of *P. chapoda*' diet in nature (G. Q. Romero, pers. obs.). The insects captured were counted, measured (total length) and identified at least to order (family when possible). The general regression equations of Hódar (1996) were used to estimate the biomass. Since some of these insects may have come from an aquatic environment adjacent to the grassland, the specimens caught were designated as "aquatic" if they were from an order or family known to develop in water during their larval period. All others were designated as "terrestrial".

STATISTICAL ANALYSIS

A randomized-block experimental design (Hurlbert 1984) was used for experiments 1 and 2, with each plant of the pair (sample unit) receiving a treatment. The numbers of spiders and bromeliads were compared between the treatments using randomized block, repeated measures ANOVA (Sokal & Rohlf 1995), in which the plant pairs were the blocks and time (samples) was the repeated factor. The blocks were the random effect and the treatments (inflorescence simulation and dry leaves) were fixed effects in the mixed-model ANOVA. Experiment 3 was done using a systematic design (see Hurlbert 1984) and the number of spiders was compared using repeated measures ANCOVA, with the initial number of spiders (pre-treatment: sample 0) as the covariate and time (samples) as the repeated factor. The number of spiders in the leaf-removal treatments (control, ¼ and ¾) over time were compared using the Dunnett's post hoc test (Sokal & Rohlf 1995), with $\alpha = 0.05$. The number and biomass of the insects collected in grassland and forest were compared using repeated measures ANOVA. The probabilities of the within subject factors for all the repeated measures analyses were corrected against sphericity using the Greenhouse-Geisser correction (G-G) (Sokal & Rohlf 1995). Prior to the tests, all the data were log or log (n + 1) transformed to homogenize the variances (Sokal & Rohlf 1995). The mean values (± 1

SE) presented in the figures and text were computed directly from untransformed data. Some instars of the spiders were not considered in some of the experiments because they were found only infrequently during the study period.

Results

Plants in which the architecture was changed by inflorescence simulation were less frequently colonised by *P. chapoda* than control plants (Fig. 1, Table 1). In general, individuals of several age classes, including adult males, more frequently colonised plants that had not been modified by inflorescence (Fig. 1, Table 1), except that juvenile males and females occurred with similar frequency on the control and the experimental plants (Fig. 1, Table 1). Adult+subadult females and eggsacs were more abundant on the control plants (Fig. 1, Table 1). During this experiment, the number of spiders per plant varied temporally, generally increasing at the start and decreasing at the end of the experiment (Fig. 1, Table 1).

Grassland bromeliads with dry leaves in their rosettes were less frequently colonised by *P. chapoda* (Fig. 2, Table 2). These dry leaves specifically affected adult+subadult females and young (Fig. 2, Table 2). Although adult+subadult females occurred on plants blocked with dry leaves, they were found in this microhabitat only during the first two sampling periods and then abandoned it (Fig. 2). These females (adults) did not produce eggsacs in this microhabitat (Fig. 2). In the forest, only one individual of *B. balansae* from which the dry leaves had been removed (experimental groups) was colonised by a young *P. chapoda* (i.e., in only one sampling period); none of the bromeliads with dry leaves in their rosette (control groups) were colonised by this spider. The colonisation of *B. balansae* by

P. chapoda during experiments 1 and 2 was very rapid (within 10-15 days spiders of all age classes had already occupied the plants). In this short interval, the adult females had also produced eggsacs on these plants.

Leaf cutting negatively affected the density of *P. chapoda* on *B. balansae* (Fig. 3, Table 3). However, this effect was seen only for plants in which three-quarters of the leaf length had been removed relative to control plants, while there was no statistically significant difference between plants that lacked one-quarter of leaf length and control plants (Dunnett's post hoc test: control vs. ¾ removed: $P = 0.004$; control vs. ¼ removed: $P = 0.296$). When data for each instar were analysed, there was no evidence that the loss of surface area in their microhabitats affected adult+subadult females and young (Table 3). Most females on the plants that lost three-quarters of their leaf length (n = 9; 78%) were on their eggsacs.

The biomass of terrestrial arthropods, and of aquatic arthropods that invaded the terrestrial environment as adults (especially chironomid dipterans) was 1.5- to 18-fold higher in grassland than in forest (Fig. 4, Table 4). Overall, 26% of the biomass of arthropods collected in grassland came from an aquatic environment, whereas only 2% of this biomass occurred in the forest. The number of terrestrial and aquatic arthropods was significantly higher in grassland than in forest (Fig. 4, Table 4).

Discussion

Changes in the rosette architecture of *B. balansae* during inflorescence affected the colonisation of plants by *P. chapoda*. Upon blooming, the plants fold their leaves back and extend them parallel to the ground, and this changed the plant architecture from a conical tridimensional configuration to a flattened, almost bidimensional one. The functional significance of these changes for the bromeliads may be to give pollinators, such as humming birds, better access. However, at the same time, these changes appear to make the bromeliad less suitable for the spider through various mechanisms. First, when the plant alters its architecture, adult and immature spiders lose the shelter at the base of the rosette and most likely become more exposed to adverse climatic conditions and to predation. The funnel shape of *B. balansae* in vegetative phase and the presence of large spines on the leaves probably make these plants a very suitable structure of protection against vertebrate predators such as birds and small mammals. Second, architectural changes alter the spider's reproduction and oviposition sites. Females of *P. chapoda* place their eggsacs in the more internal layers of the plant. This placement protects their eggs against natural enemies and desiccation, and it may facilitate nursery localisation (centre of the bromeliads) by the spiderlings (Romero & Vasconcellos-Neto, in press, a). With the leaves inclined and the central inflorescence exposed, females lost their oviposition sites and the spiderlings lost their nursery. In addition, males court females in the upper region of the vertical leaves, with the females attending in the lower region of the same leaves (Rossa-Feres *et al*. 2000). This suggests that an architectural change of the leaves to an horizontal position disrupts mating. Finally, architectural changes can affect the foraging sites. The funnel-shape tridimensional architecture of *Bromelia balansae* may channel inwards the potential prey of *P. chapoda* that have fallen into the bromeliad. These potential prey may include other jumping spiders, web-building spiders, planthoppers (homopterans), flies (dipterans), dragonflies, moths and wasps, all of which we have seen *P. chapoda* feeding on in nature (G.Q. Romero, unpublished data).

Dry leaves in the rosettes of grassland *B. balansae* also affected the colonisation of the microhabitats. Although adult females colonised bromeliads with dry leaves, they subsequently migrated and did not construct eggsacs in these plants. The presence of dry leaves probably reduces the availability of shelter for adult spiders and entirely eliminates the nursery (centre of the bromeliads) of the spiderlings.

Other studies have shown that web-building spiders (Figueira & Vasconcellos-Neto 1993) and sit-and-wait spiders that do not build webs (Fritz & Morse 1985; Morse 1990, 1992, 1993) evaluate oviposition sites and choose the more suitable sites. Evidently females of *P. chapoda* make similar oviposition-site decisions.

Our results partly corroborated an earlier hypothesis (Romero & Vasconcellos-Neto, in press, a) that *P. chapoda* does not occur in forest because dry leaves from trees block the plant base used as shelter. However, forest bromeliads from which dry leaves had been removed were not colonised, suggesting that other factors must affect the presence of spiders on these bromeliads. Since the biomass and the number of arthropods available in grassland were several fold higher than in forest, it is possible that habitat structure and prey availability may exert an additive effect on the spatial distribution of this spider population. Halaj *et al.* (1998) reported that spider abundance and species richness correlated positively with prey availability and habitat complexity. They suggested that these two factors played an important role in the community structure of spiders. However, Rypstra (1983) showed experimentally that prey availability was more important in determining the carrying capacity of a substrate for populations of the spider *Achaearanea tepidariorum* (Theridiidae), and McNett & Rypstra (2000) demonstrated experimentally that habitat complexity was a primary factor in determining habitat (plant species) selection by a web-building spider, *Argiope trifasciata* (Araneidae). These divergent findings (see also Greenstone 1984) illustrate the need for more experimental studies on spiders from different guilds before we can draw general conclusions about the relative importance of prey availability versus habitat structure in determining spider distribution.

For the spiders, the base of the bromeliad rosettes is a useful shelter and the leaf surface provides a foraging sites. Changes in both of these structures affected how long the spiders stayed on plants. In grassland, there are more individuals of *P. chapoda* on plants with larger leaves (Romero & Vasconcellos-Neto, in press, a). Prey may be more likely to land on the leaves of larger plants (i.e., large leaves may be better foraging sites for the spiders). However, analysis for each spider phenophase showed that cutting the leaves did not affect the number of adult+subadult females and young. Most of the adult females found on plants that had lost tree-quarters of their leaf length were on eggsacs and possibly remained on the plants to protect their offspring. Moreover, since the young (4th and 5th instars) are small, the loss of surface area did not affect them. In addition, to abandon the microhabitat in this phenophase might involve a high risk of mortality through predation or desiccation during migration.

In our experiments, *Psecas chapoda* colonised the bromeliads rapidly and individuals of almost all ages occupied the plants with unaltered architecture (without inflorescence or dry leaves), suggesting that they had a high efficiency in encounters with the host plant, and that they were capable of recognising and evaluating the physical state of the microhabitat. This efficiency in locating the host plant may reflect an adaptation of these spiders to the plant and may have favoured the occupation of *B. balansae* by *P. chapoda* in different regions. Indeed, *Psecas chapoda* inhabits *B. balansae* in at least three South American countries (Höfer & Brescovit 1994; Rossa-Feres *et al*. 2000; Romero & Vasconcellos-Neto, in press, a, b; G.Q. Romero, unpublished data), indicating a strong association between this spider and a bromeliad species. Juvenile males and females (antepenultimate instar) colonised with similar frequency the control and experimental plants in various experiments. Spiders of this age may have moved frequently among the bromeliads in search of suitable microhabitats, without older and larger spiders (adults or subadults) to prey on or expel them (G.Q. Romero, personal observation), with spiders in this instar remaining on any bromeliads until more suitable bromeliads are abandoned by older spiders. However, little is known about migration of spiders of different ages among bromeliads and levels of intraspecific competition among the different age groups.

In conclusion, the way bromeliad architecture changes during inflorescence appears to make the plants less suitable for *P. chapoda*. Dry leaves falling from trees also appear to affect the colonisation of the bromeliads in the forest. Since prey availability was much higher in the grassland than in the forest, microhabitat structure and prey availability may be additional factors that shape the spatial distribution of *P. chapoda* populations. The several aspects that characterise the association of *P. chapoda* with *B. balansae* (microhabitats for shelter, foraging, mating and oviposition) appear to be strictly dependent on phytosociological parameters such as the size, morphology and habitat of the bromeliads. Alterations in these microhabitats can lead to instability in this spider-plant association.

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Table 1. Randomised block, repeated measures ANOVA examining the effects of *Bromelia balansae* inflorescence simulation (treatment) on colonisation by *Psecas chapoda* and on the occurrence of eggsacs.

Parameters	Source of variation	df	MS	*F*	*P*	*G-G*
Total						
	Treatment	1	1.220	12.13	0.002	
	Error	25	0.101			
	Time	3	0.164	7.00	<0.001	<0.001
	Time x treatment	3	0.016	0.70	0.558	0.551
	Error	75	0.023			
Females (adults+ subadults)	Treatment	1	0.449	16.17	<0.001	
	Error	25	0.028			
	Time	3	0.047	3.24	0.027	0.028
	Time x treatment	3	0.023	1.56	0.206	0.208
	Error	75	0.015			
Males (adults)						
	Treatment	1	0.098	7.63	0.011	
	Error	25	0.013			
	Time	3	0.029	2.85	0.043	0.049
	Time x treatment	3	0.010	0.94	0.425	0.418
	Error	75	0.010			
Males + females (juveniles)	Treatment	1	0.011	1.20	0.284	
	Error	25	0.009			
	Time	3	0.016	1.70	0.181	0.182
	Time x treatment	3	0.005	0.55	0.652	0.650
	Error	75	0.009			
Young						
	Treatment	1	0.881	9.78	0.004	
	Error	25	0.090			
	Time	3	0.049	1.93	0.132	0.136
	Time x treatment	3	0.014	0.56	0.645	0.637
	Error	75	0.025			
Eggsacs						
	Treatment	1	0.214	7.86	0.010	
	Error	25	0.027			
	Time	3	0.045	4.67	0.005	0.007
	Time x treatment	3	0.018	1.86	0.143	0.152
	Error	75	0.010			

Table 2. Randomised block, repeated measures ANOVA examining the effects of the dry leaves added to the rosettes of *Bromelia balansae* (treatment) on the colonisation by *Psecas chapoda*.

Parameters	Source of variation	df	MS	*F*	*P*	*G-G*
Total						
	Treatment	1	1.743	30.76	<0.001	
	Error	17	0.057			
	Time	3	0.025	0.94	0.430	0.422
	Time x treatment	3	0.021	0.78	0.508	0.495
	Error	51	0.027			
Females (adults+ subadults)	Treatment	1	0.271	8.06	0.011	
	Error	17	0.034			
	Time	3	0.038	4.12	0.011	0.020
	Time x treatment	3	0.008	0.885	0.455	0.432
	Error	51	0.009			
Young						
	Treatment	1	0.801	30.75	<0.001	
	Error	17	0.920			
	Time	3	0.063	2.471	0.072	0.073
	Time x treatment	3	0.037	1.44	0.242	0.243
	Error	51	0.026			

Table 3. Repeated measures ANCOVA examining the effects of leaf removal (¼ and ¾ of the total length) in *Bromelia balansae* (treatment) on the permanence of *Psecas chapoda*. The initial number of spiders was the covariate.

Parameters	Source of variation	df	MS	*F*	*P*	*G-G*
Total						
	Treatment	2	0.783	11.64	<0.001	
	Covariate	1	0.669	9.935	0.004	
	Error	26	0.067			
	Time	5	0.022	1.21	0.306	0.309
	Time x treatment	10	0.025	1.38	0.195	0.214
	Error	130	0.018			
Females (adults+ Subadults)	Treatment	2	0.145	2.25	0.126	
	Covariate	1	0.206	3.19	0.086	
	Error	26	0.065			
	Time	5	0.031	2.61	0.027	0.049
	Time x treatment	10	0.008	0.70	0.725	0.669
	Error	130	0.012			
Young						
	Treatment	2	0.119	2.07	0.146	
	Covariate	1	0.012	0.21	0.650	
	Error	26	0.058			
	Time	5	0.005	0.24	0.943	0.914
	Time x treatment	10	0.036	1.60	0.115	0.135
	Error	130	0.023			

Table 4. Repeated measures ANOVA examining the biomass (mg) and the number of terrestrial and aquatic arthropods (prey availability) in grassland and forest (environment).

Parameters	Source of variation	df	MS	*F*	*P*	*G-G*
Biomass of arthropods						
	Environment	1	27.200	42.81	<0.001	
	Error	18	0.635			
	Time	3	0.501	0.17	0.414	0.411
	Time x environment	3	0.175	0.34	0.798	0.787
	Error	54	0.517			
No. of arthropods						
	Environment	1	4.929	110.09	<0.001	
	Error	18	0.045			
	Time	3	0.152	3.56	0.020	0.024
	Time x environment	3	0.137	3.20	0.030	0.035
	Error	54	0.043			

Figure captions

Fig. 1. Number of spiders in each age class and the number of eggsacs of *Psecas chapoda* on individuals of *Bromelia balansae* with (black circles) and without (open circles) inflorescence simulation (see methods for details). Beginning of the experiment: Oct. 5, 2001; samples: 1 = Oct. 20, 2001, 2 = Nov. 2, 2001, 3 = Nov. 21, 2002, 4 = Dec. 8, 2001. Error bars are ± 1 SE.

Fig. 2. The total number of spiders, and the number of adult+subadult females, young and eggsacs of *Psecas chapoda* on individuals of *Bromelia balansae* that received (black circles) or did not received (open circles) dry leaves in their rosette (see methods for details). Beginning of the experiment: Sep. 20, 2002; samples: 1 = Sep. 30, 2002, 2 = Oct 15, 2002, 3 = Oct 26, 2002, 4 = Nov. 9, 2002. Error bars are ± 1 SE.

Fig. 3. The total number of spiders, and the number of adult+subadult females and young *Psecas chapoda* on individuals of *Bromelia balansae* without (black circles) and with partial leaf removal (black square = ¼ removal; open triangles = ¾ removal) to reduce leaf length. Beginning of the experiment (sample 0): Dec. 30, 2002; samples: 1-5 = Dec. 31, 2002 to Jan. 4, 2003; 6 = Jan. 18, 2003. Error bars are ± 1 SE.

Fig. 4. Biomass and number of terrestrial + aquatic (when in larval phase) arthropods collected with sticky traps in grassland (open circles) and adjacent forest (closed circles). Samples: 1 = Nov. 9, 2002, 2 = Nov. 23, 2002, 3 = Jan. 8, 2003, 4 = Feb. 12, 2003. Error bars are ± 1 SE.

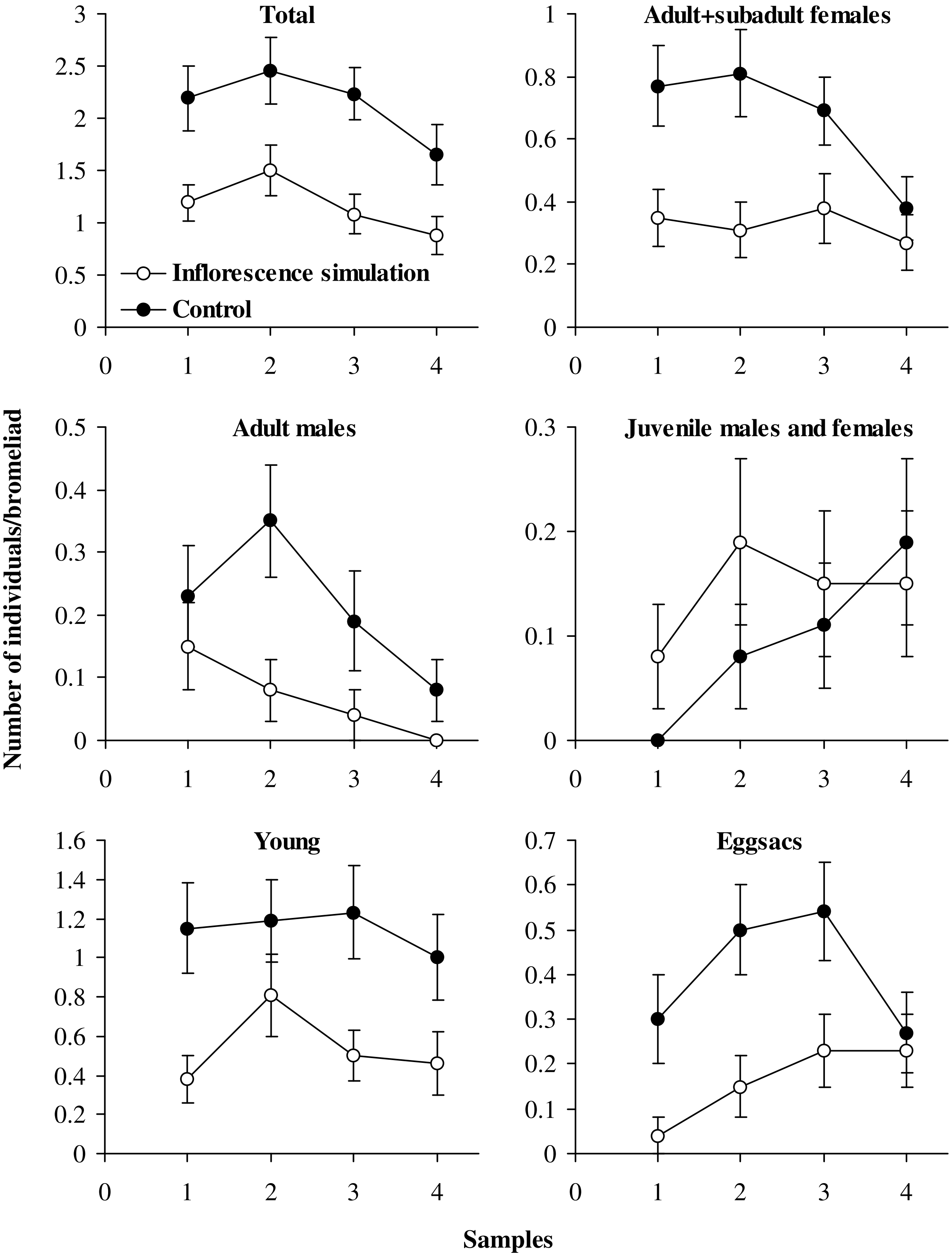

Total
Adult+subadult females
Adult males
Juvenile males and females
Young
Eggsacs
Inflorescence simulation
Control
Number of individuals/bromeliad
Samples
0
1
2
3
4
0
0.5
1
1.5
2
2.5
3
0.2
0.4
0.6
0.8
0.1
0.3
0.5
1.2
1.4
1.6
0.7

Fig. 1.

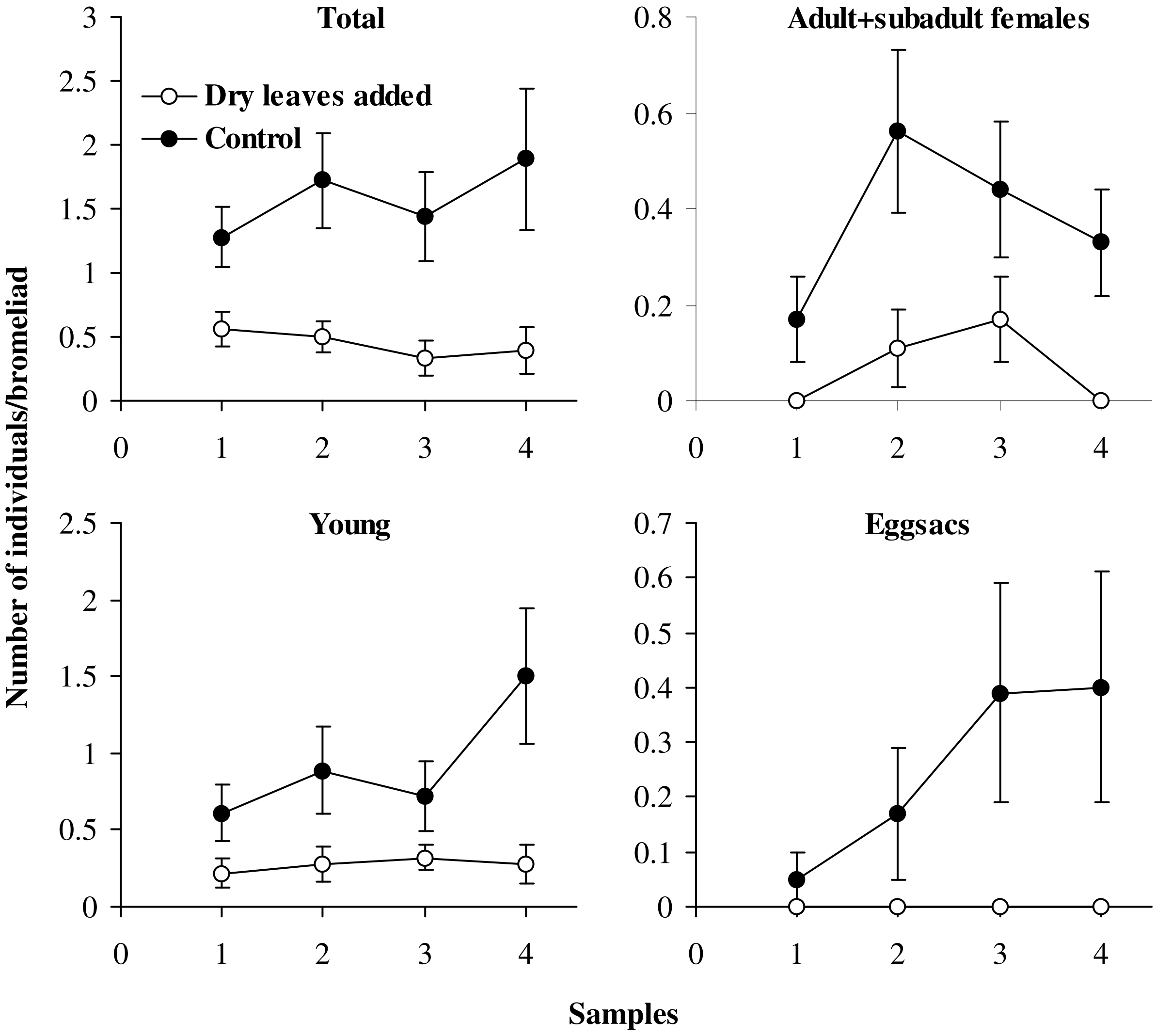

Total
Dry leaves added
Control
Adult+subadult females
Young
Eggsacs
Number of individuals/bromeliad
Samples
3
2.5
2
1.5
1
0.5
0
0.8
0.6
0.4
0.2
0.7
0.5
0.3
0.1
0
1
2
3
4

Fig. 2.

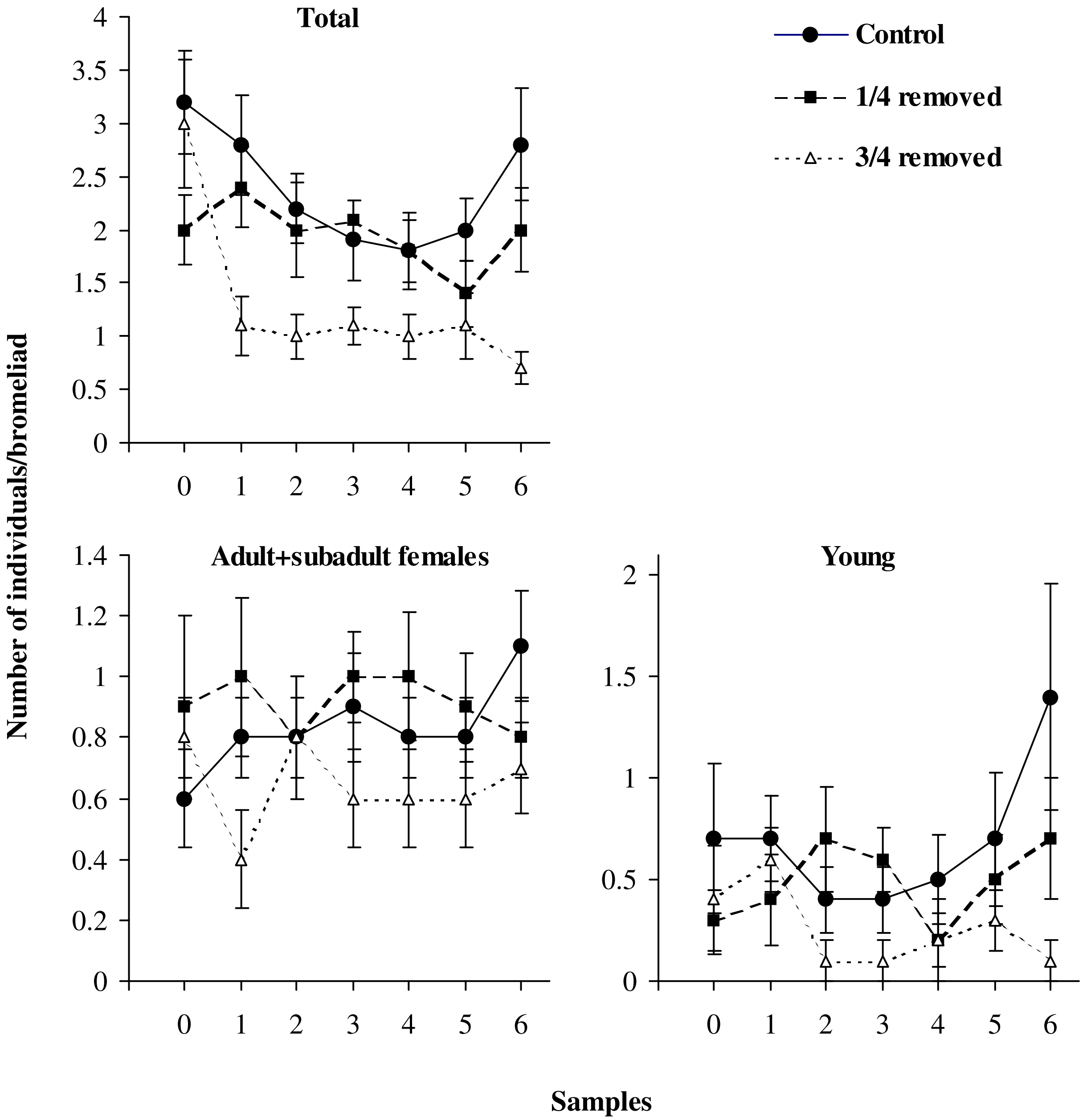
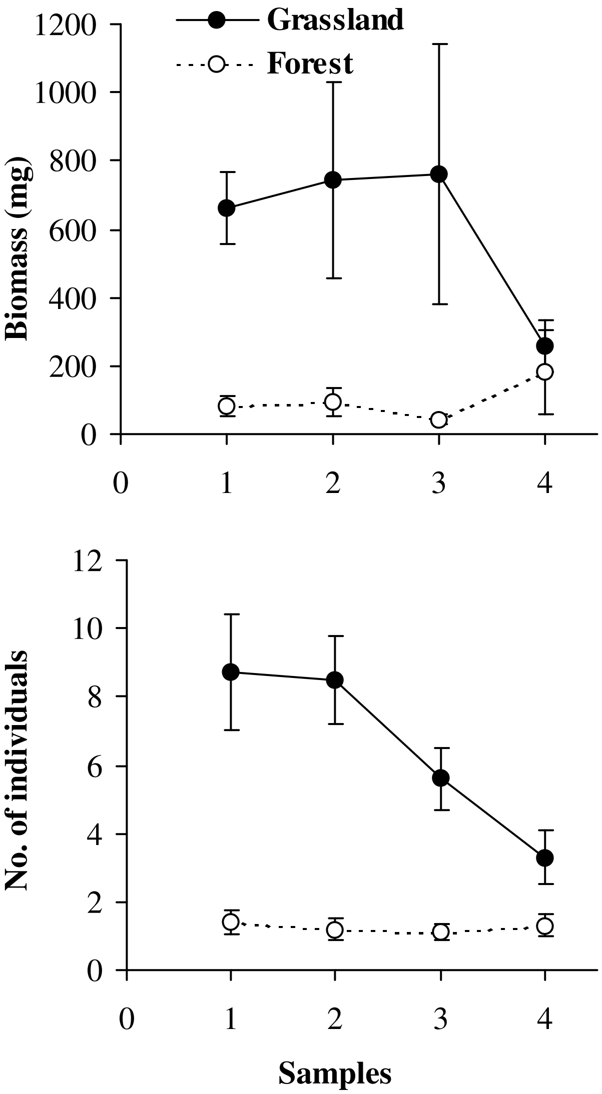

Total
Control
1/4 removed
3/4 removed
Adult+subadult females
Young
Number of individuals/bromeliad
Samples
0
0.5
1
1.5
2
2.5
3
3.5
4
0.2
0.4
0.6
0.8
1.2
1.4
1
2
3
4
5
6

Fig. 3.



Grassland
Forest
Biomass (mg)
1200
1000
800
600
400
200
0
0
1
2
3
4
No. of individuals
12
10
8
6
4
2
0
0
1
2
3
4
Samples

Fig. 4

Artigo 6

Manuscrito não publicado

Geographic range, habitats and host plants of bromeliad-living jumping spiders (Salticidae)

Running title: Bromeliad-dwelling jumping spiders

Abstract

Although spiders are a very diverse group on vegetation, their associations with plants are poorly known. Some salticid species specifically use Bromeliaceae as host plants in some regions of South America. In this study, I report the geographic range of these bromeliad-dwellers, and whether they inhabit particular bromeliad species and vegetation types, as well as open areas or interior of forests. Nine salticid species were found to be associated with up to 23 bromeliad species in cerrados (savanna-like vegetation), semideciduous and seasonal forests, coastal sand dune vegetation, restingas, inselbergs, highland forests, chacos and rain forests at 47 localities in Brazil, Paraguay, Bolivia and Argentina. Some species were typically specialists, inhabiting almost exclusively one plant species over a large geographic range (e.g., *Psecas chapoda* on *Bromelia balansae*), whereas others were generalists, occurring on up to 7-8 bromeliad species (e.g., *Psecas* sp., *Eustiromastix nativo* and *Coryphasia* sp. 1). A regional availability of bromeliad species among habitats may explain this pattern of host plant use. More jumping spiders were found on bromeliads in open areas than on bromeliads in the interior of forests. This is one of the few studies to report specific associations between spiders and plants, and possibly the first to report a host-specific geographic range for spiders on a particular plant type.

Key-words: animal-plant interactions, Bromeliaceae, distribution patterns, habitat, host plant, jumping spiders, specific associations.

Introduction

Numerous studies have shown how spiders are distributed among habitats and have suggested that they select microhabitats based on physical factors (reviewed in Wise 1993), that particular species actively select substrates with a specific architecture (Robinson 1981, Uetz 1991, Cumming & Wesolowska 2004), and that spiders have a considerable ability to select the best sites for shelter (Gunnarsson 1990, 1992), foraging (Morse 1988, 2000, Riechert & Gillespie 1986, Romero & Vasconcellos-Neto 2004a), and reproduction (Evans 1997, Taylor 1998, Taylor & Jackson 1999, Rossa-Feres *et al*. 2000). Although several spider families are known to typically live on vegetation, (Foelix 1996, Wise 1993), examples of host-specificity such as is common in herbivorous insects (Schoonhoven *et al*. 1998), are poorly known for spiders. However, recent studies have shown that spiders inhabit and breed on specific plant groups (Figueira & Vasconcellos-Neto 1991, Baurecht & Barth 1992, Taylor 1998, Taylor & Jackson 1999, Rossa-Feres *et al*. 2000, Dias & Brescovit 2003, 2004, Romero & Vasconcellos-Neto 2004a,b, 2005a,b,c), which suggests that such interactions could be a fruitful area for future research.

In South and Central America, associations between spiders and the Bromeliaceae may be especially common. All known species of the tropical wandering spiders of the genus *Cupiennius* (Ctenidae) are closely associated with particular plant groups, especially Bromeliaceae and Musaceae, on which they hide during the day and prey, court, and molt during the night (Barth *et al*. 1988a). *Cupiennius salei*, in particular, lives in close association with certain bromeliad species (Barth & Seyfarth 1979, Barth *et al*. 1988a), and exchanges vibratory courtship signals on the leaves of these plants (Barth *et al*. 1988b, Baurecht & Barth 1992). *Pachistopelma rufonigrum*, a theraphosid, and *Nothroctenus fuxico*, a ctenid, specifically inhabit tank-bromeliads in northeastern Brazil and apparently use these plants for sheltering against high temperatures in their sandy-soil habitat (Santos *et al*. 2002, Dias & Brescovit 2003, 2004).

Specific associations of jumping spiders with bromeliads have been demonstrated locally, mainly based on the observation of spider behavior (Rossa-Feres *et al*. 2000) and population dynamics on the host plant (Rossa-Feres *et al*. 2000, Romero & Vasconcellos-Neto 2005b). To date, the most thoroughly studied example of a spider-bromeliad association from the Salticidae is *Psecas chapoda* (Peckham & Peckham). This salticid associates with *Bromelia balansae* Mez. (Bromeliaceae), and courtship, mating, oviposition, and spiderling recruitment all occur on *B. balansae* (Rossa-Feres *et al*. 2000, Romero & Vasconcellos-Neto 2005b). In at least one site from southeastern Brazil (Dois Córregos city), this species occurs exclusively on *B. balansae* (Romero & Vasconcellos-Neto 2005a).

Psecas vellutinus, *Psecas* sp., and *P. splendidus* Badcock also associate with bromeliads (G. Q. Romero, unpubl. obs.), and *Eustiromastix nativo* Santos & Romero uses bromeliads for reproduction, foraging and shelter (Romero & Vasconcellos-Neto 2004b). All specimens of *E. nativo* that have been collected have come from bromeliads. *Uspachus* sp. n. has frequently been found on the bromeliad *Hohenbergia ramageana* Mez. in northeastern Brazil (Natal city), and no specimens have been found on plants other than bromeliads (Romero & Vasconcellos-Neto 2004b). *Asaphobelis physonychus* Simon and two undetermined *Coryphasia* species (*Coryphasia* sp. 1 and sp.2) also associate with bromeliads (G. Q. Romero, unpubl. obs.).

Bromeliads often provide highly suitable microhabitats for jumping spiders since their leaves form a complex tridimensional architecture (rosette) that can be used by adult and immature spiders as shelter against predators or harsh climatic conditions, as well as for foraging, mating and egg laying (Rossa-Feres *et al*. 2000, Romero & Vasconcellos-Neto 2004b, 2005a,b,c), and as nursery for spiderlings (Romero & Vasconcellos-Neto 2005a). However, except for *Psecas chapoda*, there is little information on the natural history of bromeliad-associated salticids. In the present study, the following questions were addressed: 1) Are bromeliad-living jumping spiders only locally associated with bromeliads or do they have a host-specific geographic distribution? 2) Does each salticid species inhabit a specific vegetation type (phytophysiognomy)? 3) Does each spider species inhabit particular bromeliad species or bromeliads with a specific type of architecture (e.g., presence or absence of phytotelmata)?, and 4) Do these spiders occur on bromeliads in open and/or forested areas?

Material and methods

Data on the association between jumping spiders and bromeliads were obtained from direct observations in the field, but were supplemented by information from the literature and from museum specimens. The sites for field observations (August 1996 to

April 2005) were chosen mainly based on their accessibility and on the availability of substrata (bromeliads), but covered a wide range of habitats in South America and included a variety of phytophysiognomies (Tables 1 and 2). The information recorded for each bromeliad found included the genus/species, the location of the habitat (in open sunny areas or shaded forests), and the vegetation type in the habitat. The types of vegetation ('biomes') from each geographic region were classified as semideciduous forest, cerrado (savanna-like vegetation), rain forest (ombrophitic dense forest), seasonal forest, chaco (predominantly xerophytic deciduous forests), and caatinga (xeric vegetation from northeastern Brazil, dominated by cacti, bromeliads and trees with a shrubby appearance), as defined by IBGE (1993) and Davis *et al*. (1997). The vegetation surrounded by a matrix of rain forest were classified as restinga (i.e., communities on sandy soil close to the shore dominated by cacti, bromeliads, herbs and small shrubs) (Lacerda *et al*. 1984), nativo vegetation (similar to restinga, but far from the shore) (Jesus 1988, Peixoto & Gentry 1990), dune vegetation, ombrophitic, dense, high-montane forest, inselberg and intertidal zone. Rupestrian fields (i.e., open-rock pioneer vegetation) (Menezes & Giulietti 1986, Davis *et al*. 1997), here surrounded by a matrix of cerrados and seasonal forests, were also examined for possible associations between the Salticidae and the Bromeliaceae.

Each bromeliad was identified and classified into one of two general groups based on its architecture, namely, i) plants that did not accumulate rain water (type N plants, which generally had long, narrow leaves, e.g., *Bromelia* and *Ananas*) and ii) plants that accumulated rain water (type W plants; tank-bromeliads that generally had short, wide leaves, e.g., *Aechmea*, *Vriesea*, *Neoregelia*, *Hohenbergia*, *Nidularium* and *Alcantarea*). More than 6,100 bromeliads belonging to as many as 23 species were inspected in Brazil, Paraguay, Bolivia and Argentina. Only terrestrial bromeliads or epiphytes up to 1.5 m in height were considered. *Paepalanthus bromelioides* (Eriocaulaceae) and a species of Agavaceae, which have a morphology similar to the Bromeliaceae, as well as some monocotyledons bearing long, narrow leaves (e.g., sugarcane and *Pennisetum* sp.), were also inspected. For each site, the leaves and the center of the rosettes of each bromeliad were inspected and, when a jumping spider was found, its genus/species was recorded. Some spiders were collected and preserved in 70% ethanol or, when young, were maintained alive in the laboratory until adult phase for later identification. Voucher specimens were deposited in the arachnological collection of the Laboratório de Artrópodes Peçonhentos, Instituto Butantan, in São Paulo. Some museum specimens of *Psecas* (material for a revision of the genus *Psecas*) that had been collected on bromeliads (indicated on the label as: *Psecas* sp. from Cabo Frio, Rio de Janeiro, Museu Nacional do Rio de Janeiro, MNRJ 3827; *P. splendidus* from Salta, Museo Argentino de Ciencias Naturales, MACN; personal communication by M. Ramirez: *P. splendidus* from Las Gamas, Museo Argentino de Ciencias Naturales, MACN) and on a sugarcane plantation (*P. vellutinus* from Bolivia, Florida State Collection of Arthropods, FSCA) were also included. However, no ecological data (e.g., bromeliad species, habitat, etc.) were available for these museum specimens (see Table 1).

Results

Geographic range – The jumping spiders were geographically associated with Bromeliaceae in South America (Table 1, Fig. 1). The most common bromeliad-dweller was *Psecas chapoda*, which occurred at 28 localities (26 in Brazil, four states, and in one each in Paraguay and Bolivia). *Psecas chapoda*, *P. vellutinus*, *P. splendidus* and

Asaphobelis physonychus inhabited only inland areas, whereas *Psecas* sp. and *Coryphasia* sp. 2 were found close to the shore, on the Atlantic coast (Fig. 1). *Eustiromastix nativo*, *Uspachus* sp. n. and *Coryphasia* sp. 1 inhabited inland sites, but they were also found on the coast. At some sites, some of these spider species were sympatric (*P. chapoda* and *P. vellutinus* in southeastern Brazil, *E. nativo*, *Psecas* sp, and *Uspachus* sp. n. in Linhares city). In contrast, *Coryphasia* sp. 1, sp. 2, and *A. physonychus* were apparently allopatric with the other bromeliad-living jumping spiders (Fig. 1, Table 1).

Phytophysiognomy – Each spider species was associated with a particular habitat and phytophysiognomy (Table 1). For instance, *Psecas chapoda* and *P. vellutinus* typically inhabited bromeliads of savannas (cerrados) and the margins of semideciduous forests (Tables 1 and 2). *Psecas vellutinus* was also very common in agroecosystems, such as sugarcane plantations and pastures (both monocotyledons). In contrast, *Psecas* sp. occurred in the Atlantic rain forest, being found in sandy, open environments and inside forests, and *P. splendidus* occurred in regions of chaco. *Eustiromastix nativo* and *Uspachus* sp. n. inhabited sandy environments, such as restingas and nativo vegetation surrounded by a matrix of rain forest. *Asaphobelis physonychus* occurred exclusively in rain forests. *Coryphasia* sp. 1 occurred in rocky environments and inhabited highland regions, such as highland forests (elevation 1100-2000 m, in the cities of Jundiaí and Monte Verde) and inselbergs on mountain tops (elevation >2000 m, in Monte Verde city). However, this species was also found in a coastal sand dune from southern Brazil (Table 1). Like *Coryphasia* sp. 1, *Coryphasia* sp. 2 also occupied rocky environments close to sea level, in an altitudinal gradient from intertidal to inselberg (highland) areas at Sugarloaf Mount (Pão de Açúcar), Rio de Janeiro state (Table 1). This species was also found in a sandy environment (restinga) on an Atlantic island (Table 1).

Specificity for bromeliads – Whereas some salticids were species-specialists, inhabiting only one or a few plant species, others occurred on several bromeliad species (Table 1). In addition, each salticid species apparently inhabited bromeliads with a particular architecture (type N or W). *Psecas chapoda* was typically a specialist that inhabited almost exclusively *Bromelia balansae*, but also inhabited (at a low frequency) pineapples *Ananas* sp. from plantations and *Aechmea distichantha* at three of the 28 sites of occurrence (*Ananas*: Dois Córregos and Brotas; *A. distichantha*: Derrubadas; Table 1). In the areas where *P. chapoda* occupied other plant species, *B. balansae* was also present and was occupied by this spider (Table 1). *Psecas vellutinus* also inhabited *B. balansae*, and occasionally shared host plants with *P. chapoda* at some localities (G. Q. Romero, pers. obs., Table 1). In addition, *Psecas vellutinus* was found inhabiting *Ananas* sp. and two other non-native monocotyledons, as well as a type of "elephant-grass" (*Pennisetum* sp.) and, especially, sugarcane from plantations (Table 1); none of these plants accumulated rain water in their leaf axils.

Psecas chapoda and *P. vellutinus* typically inhabited bromeliads that did not accumulate rain water (type N plants). In contrast, *Psecas* sp. was a generalist, occurring on at least seven bromeliad species that accumulated rain water (type W). *Eustiromastix nativo* was also a generalist, and used at least seven species, all tank-forming bromeliads (type W). Although *B. balansae* was also present in areas where *Psecas* sp. and *E. nativo* occurred (see Table 2), it was not inhabited by these spiders. *Uspachus* sp. n. and *Asaphobelis physonychus* inhabited two and one type-W bromeliad species, respectively (Table 1). *Coryphasia* sp. 1 was apparently the most generalized species and inhabited six type-W and two type-N plants, one bromeliad and one species of Agavaceae (Table 1). No other bromeliad species were found at the site where *Coryphasia* sp. 1 inhabited the type-N bromeliad (*Bromelia antiacantha*) (Table 1). However, in areas with bromeliad species having both types of architecture (e.g., sandy dunes from Florianópolis city), *Coryphasia* sp. 1 occurred on type-W instead of type-N bromeliads (*B*. aff. *balansae*) (Tables 1 and 2). *Coryphasia* sp. 2 inhabited four type-W bromeliad species (Table 1).

Sunny or shaded environments – Most spider populations inhabited open areas (Table 1). In some regions, no bromeliad-dwellers were found, and most of the bromeliads inspected (60%) were inside forests (Table 2). Several uninhabited bromeliads were found in open areas that had phytophysiognomies with which no salticid-bromeliad associations have been found (e.g., Presidente Figueiredo, Alter do Chão, Santana do Riacho, Cariri; Table 2, Fig. 1). In addition, several bromeliads from open areas uninhabited by the salticids were type-N plants and occurred in regions (close to the coast: São Sebastião, Ubatuba, Trancoso, Florianópolis) from which spiders that use this type of plant architecture were absent (e.g., *P. chapoda*, *P. vellutinus*, Table 2, Fig. 1). In contrast, *Psecas* sp. and *Coryphasia* sp. 2 apparently occupied bromeliads from open areas and forests indiscriminately, and *A. physonychus* apparently lived only on bromeliads from inside forests (Table 1).

Discussion

The results of this study show that South American bromeliad-living jumping spiders are geographically associated with the Bromeliaceae, with some species having a host-specific distribution (e.g., *P. chapoda* on *B. balansae*). These findings, along with previous studies (Romero & Vasconcellos-Neto 2004b, 2005a,c), suggest that *P. chapoda*, *Psecas* sp. and *E. nativo*, in particular, are strongly associated with the Bromeliaceae. Although a high level of specificity for host plants and host-specific distributions is common among herbivorous insects (see Schoonhoven *et al*. 1998), reports of similar specificity is unusual for predaceous arthropods (but see Sloggett & Majerus 2000 for an example). In the Neotropics, bromeliads are an especially abundant, diverse plant group (Benzing 2000), and their rosette-shaped structure is distinctive. The bromeliad-living salticids have apparently adapted to exploit this distinctive and common South American microhabitat (Rossa-Feres *et al*. 2000, Romero & Vasconcellos-Neto 2004b, 2005a,b,c, Romero et al., unpublished data). The findings that unrelated genera were bromeliad-dwellers suggest that bromeliad specialization by jumping spiders has evolved independently more than once. However, some genera (*Psecas* and *Coryphasia*) contained more than one bromeliad-living species. The related species of each genus may have speciated and then occupied the bromeliads in different geographic regions. Alternatively, a bromeliad-dwelling ancestor of each *Psecas* and *Coryphasia* may have radiated and speciated among the bromeliads in different geographic regions. Future phylogenetic analyses will help to solve this question.

Although some jumping spiders appeared to specialize by inhabiting almost exclusively one host species (e.g., *P. chapoda* on *Bromelia balansae*), others were generalists that occurred on several plant species. This phenomenon may reflect the availability of host plant species across the different habitats (phytophysiognomies) in different geographic regions. The areas in which *P. chapoda* occurs are generally characterized by savanna and semideciduous forests, which are habitats dominated by *B. balansae* (Smith & Downs 1979, G.Q. Romero, pers. obs.), a terrestrial species with long, narrow leaves that does not accumulate rain water (type-N plant). Other jumping spiders were found in areas in which the bromeliad flora was especially rich and diverse. This was particularly the case close to coastal rain forests (Smith & Downs 1979, Fontoura *et al*.

1991, Por 1992, Benzing 2000, G.Q. Romero, unpubl. obs.). The bromeliads (e.g. *Aechmea*, *Vriesea*, *Neoregelia*, *Hohenbergia*, and *Nidularium*) in these habitats typically have short, wide leaves that form a tank in which rain water accumulates (type-W plants) (Benzing 2000). The similar morphology of these different bromeliad species may account for why the bromeliad-dwelling salticids in these habitats associate with several, instead of any one, species.

In general, the spiders that inhabited type-W bromeliads did not occur on type-N bromeliads, even in areas where both types of bromeliads were sympatric. For instance, *Coryphasia* sp. 1 occurred on type-N bromeliads in areas in which type-W bromeliads were absent, whereas in areas in which both bromeliad types were present, these spiders occurred exclusively on type-W bromeliads. These findings suggest that some bromeliad-living salticids may often have a preference for tank-forming bromeliads. The water that accumulates in tank-bromeliads may be an important resource in protection against harsh climatic conditions or as a shelter against predators. The anti-predator advantage of these plants was suggested by the behavior of *Psecas* sp., *E. nativo*, and *Coryphasia* spp. in submerging themselves inside the bromeliads' phytothelmata in response to the approach of an observer (Romero & Vasconcellos-Neto 2004b, G.Q. Romero *et al.*, unpubl. obs.). Definite conclusions about host-plant selection were not possible for most populations of salticids that inhabited type-N bromeliads (*P. chapoda* and *P. vellutinus*) because the spiders tended to have no contact with type-W bromeliads. However, at one site (Derrubadas city), *P. chapoda* occurred in both bromeliad types, but was more frequently observed on *B. balansae*, suggesting that this species may choose type-N plants (Table 1). *Bromelia balansae* was characterized by long, hard thorns at the leaf margins (not commonly seen in other bromeliad species) that may function analogously to the tank in protecting spiders against predators.

Although *P. vellutinus* inhabited type-N bromeliads (*Bromelia* and *Ananas*), this species also occurred at a high frequency on other monocotyledonous plants, especially sugarcane. In other studies, several individuals of *P. vellutinus* were collected on sugarcane (Rinaldi & Forti 1997, Rinaldi *et al*. 2002). The concave shape of cane sheaths is similar to shape to type-N bromeliad leaves (G.Q. Romero, pers. obs.), which suggests that the ability of *P. vellutinus* to live on type-N bromeliads has favored this species to also use sugarcane, a species that is not native to Brazil (introduced in 1530).

In most reports of strict associations between web-building and actively hunting spiders with certain plant groups, the plants have been monocotyledons, including other bromeliads (Barth & Seyfarth 1979, Barth *et al*. 1988a,b, Baurecht & Barth 1992, Santos *et al*. 2002, Dias & Brescovit 2003, 2004), *Paepalanthus bromelioides* (Eriocaulaceae), a bromeliad-like plant (Figueira & Vasconcellos-Neto 1991), *Phormium tenax* (New Zealand flax, Liliaceae) (Taylor 1998, Taylor & Jackson 1999), Musaceae (Barth & Seyfarth 1979, Barth *et al*. 1988a,b, Baurecht & Barth 1992,), and other plants with a rosette shape (*Cordyline* spp., Agavaceae) (Taylor 1998, Taylor & Jackson 1999, R.R. Jackson, pers. commun.). Certain traits of monocotyledonous plants, such as the rosette-shape architecture of their leaves (Bromeliaceae, Agavaceae and *Paepalanthus bromelioides*), the leaf sheaths (Musaceae and larger grasses), and the large, flat leaf surface area may attract spiders to live on them.

Psecas chapoda typically occurred on *B. balansae* in open areas (Romero & Vasconcellos-Neto 2005a) and manipulative experiments have shown that dry leaves falling from forest trees block the internal base of the rosettes, thereby preventing the use of shelter and resting places by *P. chapoda* (Romero & Vasconcellos-Neto 2005c). This problem may be widely applicable, not only to other *P. chapoda* populations, but also to most bromeliad-living jumping spiders, including *E. nativo* and *Coryphasia* sp. 1 which, despite their occurrence in both open areas and forests, have been observed more often in the former (Romero & Vasconcellos-Neto 2004b, G.Q. Romero *et al*., unpublished data). At several sites with different vegetation types, forest-dwelling bromeliads of diverse species contained an accumulation of dry leaves (fallen from forest trees) in the internal base of their rosettes (G.Q. Romero, unpubl. obs.).

This study is a first step toward understanding the patterns of geographic range, habitats and host plants used by bromeliad-dwelling jumping spiders. These spiders were associated with the Bromeliaceae in a wide geographic extension, with each species generally occupying specific habitats. While some spiders were generalists, occupying up to 7-8 bromeliad species, others were specialists, inhabiting mainly one plant species. Most of the bromeliad-dwellers inhabited open areas. The associations described here between salticids and particular plant species appear to be unusual, but this might partly be because, until now, little attention has been given to spider-plant specificity. Further investigation of the plant traits that attract particular spiders will contribute to our understanding of spider-plant mutualisms and food web dynamics, and should prove useful in establishing spider inventories and in efforts to conserve spider biodiversity.

Acknowledgements

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Table 1. Geographic range, host plants and habitats of the bromeliad-dwelling jumping spiders.

Genera/Species	Host-plants	Locality [country, city (state or province)]	Plant type[T]	N[n]	Open (O) or Forested (F) areas	Vegetation types[V]
Psecas						
P. chapoda	*Bromelia balansae*	BR: São José do Rio Preto (São Paulo) *[1]	N	~200	O/F	SF
P. chapoda	*B. balansae*	BR: Jaú (São Paulo)	N	~350	O	SF
P. chapoda	*B. balansae*	BR: Bocaina (São Paulo)	N	3	O	SF
P. chapoda	*B. balansae*	BR: Brotas (São Paulo)	N	2	O	Cer
P. chapoda	*B. balansae*	BR: Botucatu (São Paulo)	N	?	O	SF
P. chapoda	*B. balansae*	BR: Dois Córregos (São Paulo) *[2]	N	~2000	O/F	SF
P. chapoda	*B. balansae*	BR: São Carlos (São Paulo)	N	32	O	SF
P. chapoda	*B. balansae*	BR: Itirapina (São Paulo)	N	15	O	Cer
P. chapoda	*B. balansae*	BR: Teodoro Sampaio (São Paulo)	N	2	O	SF
P. chapoda	*B. balansae*	BR: Santa Fé do Sul (São Paulo)	N	2	O	SF
P. chapoda	*B. balansae*	BR: Primavera (São Paulo)	N	6	O	SF
P. chapoda	*B. balansae*	BR: Presidente Epitácio (São Paulo)	N	12	O	SF
P. chapoda	*B. balansae*	BR: Aquidauana (Mato Grosso do Sul)	N	~20	O	Cer
P. chapoda	*B. balansae*	BR: Corumbá (Mato Grosso do Sul)	N	103	O	Cer
P. chapoda	*B. balansae*	BR: Coxim (Mato Grosso do Sul)	N	8	O	Cer
P. chapoda	*B. balansae*	BR: Brasilândia (Mato Grosso do Sul)	N	29	O	SF
P. chapoda	*B. balansae*	BR: Bataguassú (Mato Grosso do Sul)	N	4	O	SF
P. chapoda	*B. balansae*	BR: Santa Rita do Pardo (Mato Grosso do Sul)	N	~10	O	SF
P. chapoda	*B. balansae*	BR: Anaurilândia (Mato Grosso do Sul)	N	2	O	SF
P. chapoda	*B. balansae*	BR: Campo Grande (Mato Grosso do Sul)	N	?	O	Cer
P. chapoda	*B. balansae*	BR: Terenos (Mato Grosso do Sul)	N	?	O	Cer
P. chapoda	*B. balansae*	BR: Camapuã (Mato Grosso do Sul)	N	?	O	Cer
P. chapoda	*B. balansae*	BR: Bela Vista (Mato Grosso do Sul)	N	?	O	Cer
P. chapoda	*B. balansae*	BR: Poconé (Mato Grosso)	N	15	O	Cer
P. chapoda	*B. balansae*	BR: Chapada dos Guimarães (Mato Grosso)	N	12	O	Cer
P. chapoda	*B. balansae*	BR: Derrubadas (Rio Grande do Sul)	N	20	O	Ru (SeF)
P. chapoda	*B. balansae*	PAR: Bella Vista (Itapúa)	N	?	O	Cer
P. chapoda	*B. balansae*	BOL: ? (Beni) *[3]	N	11	O	Cer
P. chapoda	*Aechmea distichantha*	BR: Derrubadas (Rio Grande do Sul)	W	1	O	Ru (SeF)
P. chapoda	*Ananas* sp. (plantation)	BR: Dois Córregos (São Paulo)	N	2	O	Agro (Cer)
P. chapoda	*Ananas* sp. (plantation)	BR: Brotas (São Paulo)	N	1	O	Agro (Cer)
P. vellutinus	*B. balansae*	BR: Jaú (São Paulo)	N	~150	O	SF
P. vellutinus	*B. balansae*	BR: Dois Córregos (São Paulo)	N	63	O	SF
P. vellutinus	*Ananas* sp. (plantation)	BR: Jaú (São Paulo)	N	9	O	Agro (SF)

P. vellutinus	*Ananas* sp. (plantation)	BR: Linhares (Espírito Santo)	N	36	O	Agro (RF)
P. vellutinus	*Pennisetum* sp. (pasture)	BR: Campinas (São Paulo)	--	1	O	SF
P. vellutinus	Sugarcane plantation	BR: Jaú (São Paulo)	--	20	O	Agro (SF)
P. vellutinus	Sugarcane plantation	BR: Campinas (São Paulo)	--	2	O	Agro (SF)
P. vellutinus	Sugarcane plantation	BR: Batatais (São Paulo)	--	15	O	Agro (SF)
P. vellutinus	Sugarcane plantation	BR: Dois Córregos (São Paulo)	--	58	O	Agro (SF)
P. vellutinus	Sugarcane plantation	BR: Botucatu (São Paulo) *[4]	--	84	O	Agro (SF)
P. vellutinus	Sugarcane plantation	BR: Linhares (Espírito Santo)	--	5	O	Agro (RF)
P. vellutinus	Sugarcane plantation	BOL: ? (?)	--	11	O	Agro (Cer)
Psecas sp.	*Aechmea blanchetiana*	BR: Linhares (Espírito Santo) *[5]	W	32	F	RF
Psecas sp.	*A. macrochlamys*	BR: Linhares (Espírito Santo) *[5]	W	13	F	RF
Psecas sp.	*Vriesea neoglutinosa*	BR: Linhares (Espírito Santo) *[5]	W	1	O	NV (RF)
Psecas sp.	?Agavaceae sp. 1 **	BR: Salvador (Bahia)	W	1	O	Res (RF)
Psecas sp.	*Hohenbergia littoralis*	BR: Salvador (Bahia)	W	2	O	Res (RF)
Psecas sp.	*H.* aff. *salzmannii*	BR: Salvador (Bahia)	W	3	O	Res (RF)
Psecas sp.	*Aechmea* sp. 1	BR: Caravelas (Bahia)	W	?	O	Res (RF)
Psecas sp.	*Neoregelia cruenta*	BR: Ubatuba (São Paulo)	W	5	F	RF
Psecas sp.	?	BR: Cabo Frio (Rio de Janeiro)	?	1	?O	?Res (RF)
P. splendidus	?	AR: Hickman (Salta)	?	6	?	Ch
P. splendidus	?	AR: Las Gamas (Santa Fé)	?	1	O	Ch
P. splendidus	?	PAR: ? (?)	?	?	?	Ch
Eustiromastix						
E. nativo	*V. neoglutinosa*	BR: Linhares (Espírito Santo) *[5]	W	72	O	NV (RF)
E. nativo	*V. neoglutinosa*	BR: Trancoso (Bahia) *[5]	W	4	O	Res (RF)
E. nativo	*A. blanchetiana*	BR: Trancoso (Bahia) *[5]	W	62	O	Res (RF)
E. nativo	?Agavaceae sp. 1 **	BR: Salvador (Bahia)	W	11	O	Res (RF)
E. nativo	*H. littoralis*	BR: Salvador (Bahia)	W	2	O	Res (RF)
E. nativo	*H.* aff. *salzmannii*	BR: Salvador (Bahia)	W	1	O	Res (RF)
E. nativo	*H. ridleyi*	BR: Areia Branca (Sergipe)	W	~10	O	NV (RF)
E. nativo	*Aechmea* aff. *aquilega*	BR: Areia Branca (Sergipe)	W	~10	O	NV (RF)
E. nativo	*A. macrochlamys*	BR: Linhares (Espírito Santo) *[5]	W	19	F	RF
Uspachus						
Uspachus sp. n.	*Hohenbergia ramageana*	BR: Natal (Rio Grande do Norte) *[5]	W	32	O	DV (RF)
Uspachus sp. n.	*V. neoglutinosa*	BR: Linhares (Espírito Santo) *[5]	W	2	O	NV (RF)
Asaphobelis						
A. physonychus	*V. gigantea* ***	BR: Guaíba (Rio Grande do Sul) *[6]	W	11	F	RF
A. physonychus	*V. gigantea* ***	BR: Viamão (Rio Grande do Sul)	W	~50	F	RF
Coryphasia						
Coryphasia sp. 1	*Aechmea* aff. *ornate*	BR: Florianópolis (Santa Catarina)	W	26	O	DV (RF)
Coryphasia sp. 1	*Aechmea* aff. *lindenii*	BR: Florianópolis (Santa Catarina)	W	10	O	DV (RF)
Coryphasia sp. 1	*Vriesea* aff. *procera*	BR: Florianópolis (Santa Catarina)	W	3	O	DV (RF)

Coryphasia sp. 1	Agavaceae sp. 2 **	BR: Florianópolis (Santa Catarina)	N	1	O	RF
Coryphasia sp. 1	*B. antiacantha*	BR: Jundiaí (São Paulo)	N	~90	O	SF
Coryphasia sp. 1	*Aechmea distichantha*	BR: Monte Verde (Minas Gerais)	W	107	O/F	In, HM (RF)
Coryphasia sp. 1	*Vriesea bituminosa*	BR: Monte Verde (Minas Gerais)	W	6	F	HM (RF)
Coryphasia sp. 1	*Nidularium innocentii*	BR: Monte Verde (Minas Gerais)	W	1	F	HM (RF)
Coryphasia sp. 2	*Alcantarea glaziouana*	BR: Rio de Janeiro (Rio de Janeiro)	W	285	O	IZ, In (RF)
Coryphasia sp. 2	*N. cruenta*	BR: Rio de Janeiro (Rio de Janeiro)	W	11	O	IZ, In (RF)
Coryphasia sp. 2	*Quesnelia arvensis*	BR: Ilha do Cardoso (São Paulo) 'island'	W	57	F	Res (RF)
Coryphasia sp. 2	*Vriesea carinata*	BR: Ilha do Cardoso (São Paulo) 'island'	W	23	F	Res (RF)

Source: *[1] Rossa-Feres *et al*. (2000), *[2] Romero & Vasconcellos-Neto (2005a,b,c), *[3] Höfer & Brescovit (1994), *[4] Rinaldi & Forti 1997, Rinaldi *et al*. 2002, *[5] Romero & Vasconcellos-Neto (2004b), *[6] Lise & Braul-Jr. (1994).

** Plants in rosette shape (similar to *Bromelia antiacantha*); *** Epiphytes.

[T] Plant type: N = plants that did not accumulate rain water, generally bearing long, narrow leaves; W = plants that accumulated rain water, generally bearing short, wide leaves.

[n] Number of bromeliads (or stems of sugarcane and grasses) inspected containing at least one jumping spider.

[V] SF = semideciduous forest (margins), Cer = cerrado (savanna-like vegetation), RF = rain forest (ombrophitic dense forest), SeF = seasonal forest, Agro = agroecosystem, NV = nativo vegetation, Res = restinga, DV = coastal sand dune vegetation, HM = ombrophitic dense high-montane forest, Ru = rupestrian fields (rocky fields), Ch = chaco, IZ = intertidal zone, In = inselberg. Symbols in parentheses indicate the vegetation matrix.

Table 2. Localities, plant species or habitats (open area/forest) where no association of jumping spiders with Bromeliaceae was found.

Locality [country, city (state or province)]	Bromeliad species inspected	Plant type^T	No. of bromeliads inspected	Open (O) or Forested (F) areas	Vegetation types^V
BR: Capão Bonito (São Paulo)	*Bromelia balansae*	N	20	F	RF
BR: São Sebastião (São Paulo)	*Aechmea* spp.	W	125	F	RF
BR: São Sebastião (São Paulo)	*Vriesea* sp. 2	W	32	F	RF
BR: São Sebastião (São Paulo)	*B. antiacantha*	N	23	O	RF
BR: São Sebastião (São Paulo) ‘island’	*Neoregelia* sp.1	W	48	F	RF
BR: Ubatuba (São Paulo) *	*B. antiacantha*	N	15	F	RF
BR: Ubatuba (São Paulo) *	*B. antiacantha*	N	10	O	Res (RF)
BR: Onda Verde (São Paulo)	*B. balansae*	N	15	F	SF
BR: Jundiaí (São Paulo) *	*B. antiacantha*	N	33	F	SF
BR: Icém (São Paulo)	*B. balansae*	N	8	F	SF
BR: Campinas (São Paulo) *	*B. balansae*	N	22	F	SF
BR: Catas Altas (Minas Gerais)	*B. balansae*	N	96	F	SF
BR: Itatiaia (Rio de Janeiro)	*B.* aff. *balansae*	N	12	F	RF
BR: Linhares (Espírito Santo) *	*B. balansae*	N	16	F	RF
BR: Linhares (Espírito Santo) *	*B. balansae*	N	157	F	RF
BR: Trancoso (Bahia) *	*B.* aff. *balansae*	N	40	O	Res (RF)
BR: Florianópolis (Santa Catarina) *	*B.* aff. *balansae*	N	25	F	RF
BR: Florianópolis (Santa Catarina) *	*B.* aff. *balansae*	N	16	O	DV (RF)
BR: Manaus (Amazonas)	*B. tubulosa*	N	120	F	RF
BR: Presidente Figueiredo (Amazonas)	*Ananas* sp.	N	45	O	RF
BR: Presidente Figueiredo (Amazonas)	*?Aechmea* sp.	W	~15	O	RF
BR: Alter do Chão (Pará)	*Ananas* sp.	N	44	O	Agro (RF)
AR: (Corrientes)	*A. distichantha*	W	28	O	Ch
AR: (Corrientes)	*B. serra*	N	20	O	Ch
AR: (Corrientes)	*A. distichantha*	W	367	F	Ch
AR: (Corrientes)	*B. serra*	N	235	F	Ch
BR: Santana do Riacho (Minas Gerais)	*B. balansae*	N	130	O	Cer
BR: Santana do Riacho (Minas Gerais)	*Paepalanthus bromelioides* **	W	~200	O	Ru (Cer)
BR: São João do Cariri (Paraíba)	*B.* aff. *balansae*	N	150	O	Caa

*Localities where jumping spiders were found, but not on the plant species and/or in the habitat (open area/forest) indicated.

** Eriocaulaceae, a plant morphologically similar to the Bromeliaceae (Figueira & Vasconcellos-Neto 1991).

[T] Plant type: N = plants that did not accumulate rain water, generally bearing long, narrow leaves; W = plants that accumulated rain water, generally bearing short, wide leaves.

[V] SF = semideciduous forest, RF = rain forest (ombrophitic dense forest), Cer = cerrado (savanna-like vegetation), Res = restinga, DV = coastal sand dune vegetation, Ru = rupestrian fields, Ch = chaco, Agro = agroecosystem, Caa = Caatinga. Symbols in parentheses indicate the vegetation matrix.

Figure Captions

Fig. 1. Geographic range of the jumping spider species on Bromeliaceae. The legend indicates the distribution of each bromeliad-living species (see symbols). Open circles indicate regions where no associations between Salticidae and Bromeliaceae were found (cities without an asterisk in Table 2).

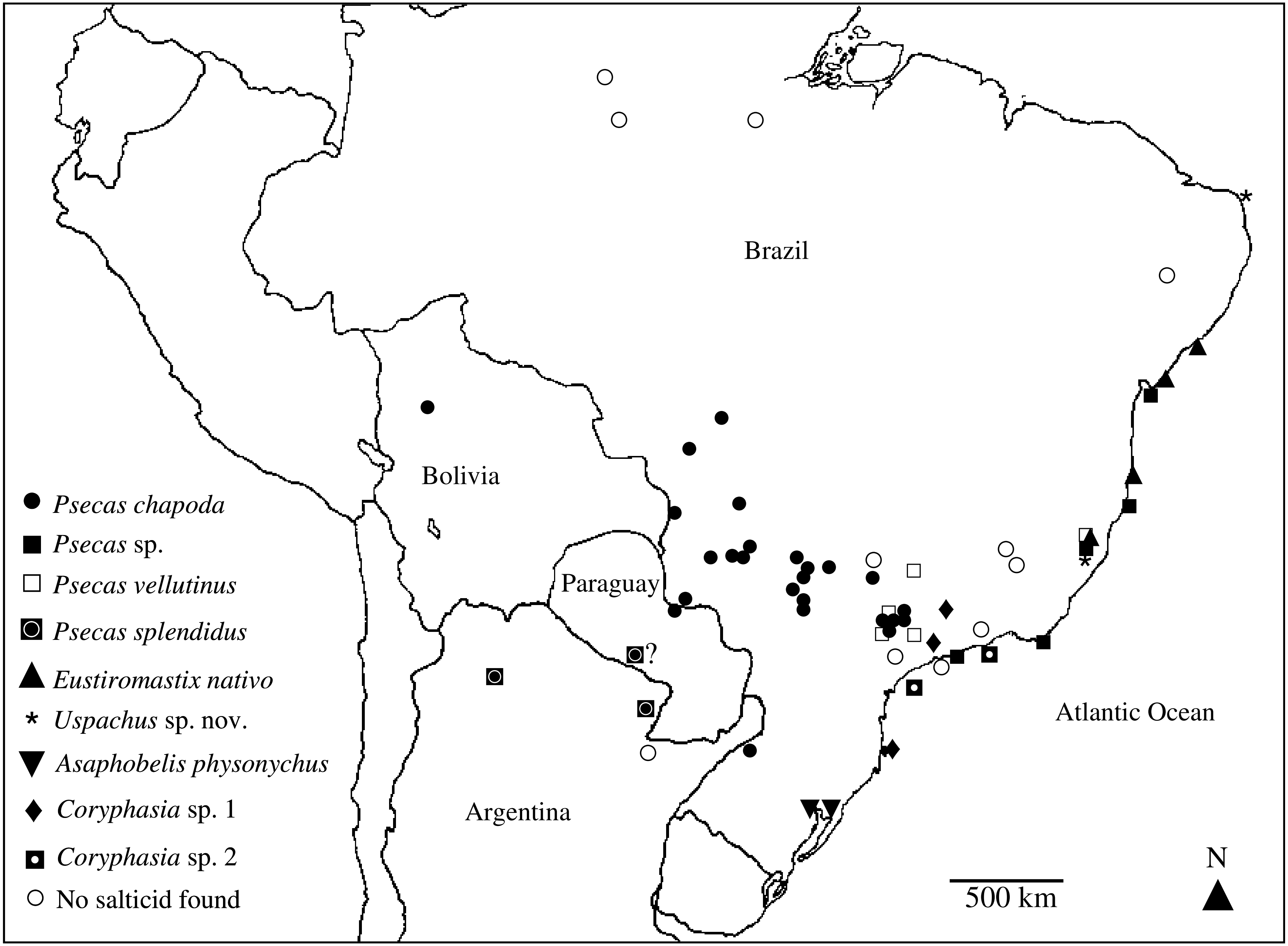
Brazil
Bolivia
Paraguay
Argentina
Atlantic Ocean
?
● Psecas chapoda
■ Psecas sp.
□ Psecas vellutinus
Psecas splendidus
▲ Eustiromastix nativo
* Uspachus sp. nov.
▼ Asaphobelis physonychus
♦ Coryphasia sp. 1
Coryphasia sp. 2
○ No salticid found
500 km
N

Fig. 1

3. MUTUALISMOS

Artigo 7

Romero, G.Q., Mazzafera, P., Vasconcellos-Neto, J. & Trivelin, P.C.O. Bromeliad-living spiders improve host plant nutrition and growth. *Ecology* (submetido).

BROMELIAD-LIVING SPIDERS IMPROVE HOST PLANT NUTRITION AND GROWTH

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Abstract. Although bromeliads are believed to obtain nutrients from debris deposited by animals in their rosettes, there is little evidence to support this assumption. Using stable isotope methods, we found that the Neotropical jumping spider *Psecas chapoda* (Salticidae), which lives strictly associated with the terrestrial bromeliad *Bromelia balansae*, contributed to 30-44% of the total nitrogen of its host plant in the field. In a one-year field experiment, plants with spiders grew 15% more than plants from which the spiders were excluded. This is the first study showing nutrient provisioning in a spider-plant system. Since several animal species live strictly associated with bromeliad rosettes, this type of mutualism involving the Bromeliaceae may be more common than previously thought.

Key words: animal-plant interaction, Bromelia balansae*, Bromeliaceae, digestive mutualism, jumping spider, nitrogen fluxes, nutrient provisioning, spider-plant mutualism,* Psecas chapoda*, Salticidae, stable isotope* ^{15}N

INTRODUCTION

Predators associated with plants can improve plant welfare by removing herbivores, as well as by provisioning host plants with nutrients derived from their debris. A vast literature has shown beneficial effects of predators to plants against herbivory. Although nutrient fluxes play a significant role in several animal-plant systems (e.g., Fischer et al. 2003, Anderson & Midgley 2003), very few studies have quantified the contribution of animals to plant nutrition, especially if the outcome of these interactions is positive to plant performance. The most known examples of animals that contribute to plant nutrition are from ant-plant systems (Huxley 1980, Rico-Gray et al. 1989, Treseder et al. 1995, Sagers et al. 2000, Fischer et al. 2003, Solano & Dejean 2004) and from mutualistic interactions involving arthropods and insectivorous plants (Ellis & Midgley 1996, Anderson & Midgley 2003).

Plants of the large Neotropical family Bromeliaceae have their leaves organized in rosettes, hence, are able to intercept and retain debris and water (Benzing 2000) from which minerals (Benzing & Burt 1970, Benzing & Renfrow 1974) and amino acids (Benzing et al. 1985, Owen-Jr & Thomson 1988, Endres & Mercier 2003) can be absorbed through specialized trichomes. Bromeliad rosettes are regularly inhabited by an extensive number of animal species (Benzing 1986, 2000), some of them being strongly dependent on the plant for foraging and reproduction (Benzing 2000). For instance, the neotropical jumping spider *Psecas chapoda* (Salticidae) inhabits and breeds strictly on the terrestrial bromeliad *Bromelia balansae*, in several regions of South America (Romero & Vasconcellos-Neto 2005a,b,c). Although nutrients derived from animal debris (i.e., feces, dead organisms and prey carcasses) are assumed to fertilize Bromeliaceae, such benefits for plant nutrition and performance have never been demonstrated.

In the present study, we used isotopic methods in greenhouse and field experiments to assess the relative contribution of the spider *P. chapoda* to the nutrition in the bromeliad *B. balansae*. The main questions addressed were: (1) Does *P. chapoda* improve *B. balansae* nutrition through its debris? (2) Does *B. balansae* grow better when inhabited by the spiders?

METHODS

Study site and organisms

The field study was carried out from April 2003 to June 2004 in fragments of semi-deciduous forest and adjacent grassland areas near Dois Córregos city (22°21′S, 48°22′W), São Paulo state, in south-eastern Brazil. Local climate consists of a distinct dry/cold (May–September) and wet/warm (October–April) season. Mean annual rainfall and mean annual temperature were 1600 mm and 21.3 °C, respectively (Romero & Vasconcellos-Neto 2005a,b). For more details of the study area see Romero & Vasconcellos-Neto (2005 a,b,c).

Bromelia balansae is a large (>1 m tall), spindly-leaved, terrestrial bromeliad common for acidic, nutrient poor cerrado (savanna-like vegetation) and semi-deciduous forest sites. The leaves of this semelparous bromeliad are concave with thorny margins, and do not form a tank to store water, but may retain a few milliliters of rainwater which would allow for extended periods of nutrient dissolution and uptake by the plant leaves. In Brazil, Bolivia and Paraguay, *B. balansae* is commonly inhabited by the host-specific jumping spider, *Psecas chapoda* (Peckham & Peckham) (Salticidae) (Fig. 1) (Romero & Vasconcellos-Neto 2005a). Each plant can harbor up to 20 mature and immature spiders (Romero & Vasconcellos-Neto 2005c). The entire life cycle of *P. chapoda*, including courtship behaviour, mating, oviposition, and spiderling recruitment occurs on the bromeliad *B. balansae* (Rossa-Feres et al. 2000, Romero & Vasconcellos-Neto 2005 a,b,c).

Spider contribution to plant nutrition in the field

Initially, we investigated the relative contribution (%N) by spiders to the nitrogen content of *Bromelia balansae* in the field by determining the natural δ^{15}N values (see below) for leaves of bromeliads growing in three areas with different spider densities: area 1 = grassland with a high spider density (mean±SE: 2.91±0.53 spiders/bromeliad), area 2 = grassland with an intermediate spider density (0.60±0.10 spiders/bromeliad), and area 3 = forest understorey with a low spider density (0.08±0.03 spiders/bromeliad). The number of spiders per bromeliad in each area was estimated by inspecting the first 10-22 bromeliads in a random 50 m x 20 m transect, and was determined four times, two in the dry season (June 19, August 28, 2004), and two in the rainy season (October 11, December 4, 2004). Areas 1 and 3 were 20-30 m apart and area 2 was ~800 m from 1 and 3. Forest bromeliads have a low spider density because dry leaves fallen from trees block the internal base of the rosettes used as shelter by this spider species (Romero & Vasconcellos-Neto 2005a). Bromeliads from area 1 were used to estimate the fraction of plant nitrogen derived from spiders, whereas bromeliads from the other two areas were used as reference plants (see equation 1).

For each area, we collected two new leaves (second node) from each of five randomly chosen non-reproductive bromeliads. Each leaf was washed for at least 3 min in running water and scrubbed by hand to eliminate contamination (organic particles and mites). The leaves were then oven-dried for 30 h at 65ºC, ground to a fine powder in a ball mill, and transferred to airtight containers. Feces from three adult female spiders were collected in the study area for isotopic determination (^{15}N). The soil nitrogen concentration (%) and soil pH did not differ among the three sites (Kruskal-Wallis test, $P \geq 0.29$).

Greenhouse experiment: nitrogen fluxes from spiders to plants

The contribution of spiders to the nutrition of *B. balansae* was investigated in the laboratory using debris obtained from spiders fed with isotopically labeled *Drosophila melanogaster* flies. The flies were cultured from eggs in a medium of agar, corn meal, glucose, minerals and ^{15}N-labeled yeast. The labeled yeast was obtained by raising commercial yeast on a Difco-Bacto carbon-based medium with 80% $(^{14}NH_4)_2SO_4$ and 20% $(^{15}NH_4)_2SO_4$ (98 atom % excess, from Cambridge Isotope Laboratories, MA) and cultured in sterile tubes at 30°C for 54 h (Schlenck & De Palma 1957). The yeast was concentrated by centrifugation, frozen, lyophilized and incorporated into the *Drosophila* medium.

To obtain spider feces and fly carcasses, 17 adult females of *P. chapoda* were maintained individually in glass jars (7 cm diameter, 11 cm high) in the laboratory, and fed 15 flies every second day. This time interval was enough for the spiders to kill all of the flies and produce feces. At 2 d intervals, the spider feces and carcasses of consumed flies were collected, lyophilized, weighed and were stored individually in polypropylene tubes. In addition, at 2 d intervals over the experiment, 15 flies were collected from the populations (jars) and received the same treatments of the feces and carcasses. The feces were collected from the jars using a micropipette and were suspended in distilled water (150 µL). Depending upon the treatment, the feces, dead flies or carcasses were deposited in the center of the rosettes of five bromeliads at two-day intervals over 48 days (from February 17 to March 4, 2004). The leaves were collected on March 11, 2004 for ^{15}N and N determinations. The bromeliads were automatically watered (fine spray) for 5 min every 8 h. This amount of water was not sufficient to remove spider debris from the pots since water did not accumulate in the plastic dish under each pot. These bromeliads were of the same cohort and were grown from seeds in pots containing homogeneous soil from the study area. Before this experiment, the plants had grown in a greenhouse for ~2.5 y and had no contact with spiders.

The potted bromeliads were small and similar in size (older leaf length ~30 cm), and corresponded to plants in the field that supported up to two adult spiders (Romero & Vasconcellos-Neto 2005c). A previous bioassay showed that adult *P. chapoda* females feed on 15-20 flies per day and produce feces continually. We surveyed and processed the leaves as previously described.

Field experiment: spider exclusion and plant growth

This experiment (May 2003-May 2004) was done at the same site used to assess the contribution of spiders to the nitrogen content of bromeliads (grassland area with a high spider density). To examine the effect of spiders on plant growth, bromeliads from the same cohort of those used in the greenhouse experiment were planted in pots (25 cm diameter, 18 cm high) containing homogeneous soil. Before this experiment, the plants had grown in greenhouse for ~2.5 y and had no contact with spiders. Sixteen bromeliads were used in each of two treatments that included plants naturally colonized by spiders (experimental group) and plants from which spiders were excluded (control group). Each bromeliad was placed on a three-legged iron support to avoid root contact with soil from the field, and the legs of the support of control plants periodically received 10 cm barriers of Tanglefoot resin (Tanglefoot Co., Grand Rapids, MI) to avoid colonization by spiders. Plants of both treatments were fixed in the soil and raised 20-30 cm above ground level. The support of plants that were to be colonized by spiders did not receive resin and were positioned so that the leaf tips touched *B. balansae* plants from the natural population to allow colonization by spiders. The control plants were randomly positioned within 1-2 m of naturally growing *B. balansae* plants and ~0.5-2 m from plants colonized by spiders. The plants were watered once a week (~ 0.5 L/week) throughout the experiment and were inspected at two-week intervals; any spider found on the control plants were removed. One new (second node) and one mature leaf (fourth or fifth node) were marked with a fine colored wire and their length was measured prior to the beginning of the experiment (May 2003), and then every three months for one year. The number of leaves per rosette was also counted throughout the experiment. Herbivory was undetectable during the experiment. All of the plants in the experimental group were rapidly colonized by spiders, as in a previous field experiment (Romero & Vasconcellos-Neto 2005a).

At the end of the experiment (May 2004), two new leaves were collected from each experimental and control rosette and prepared (as above) for isotopic analysis.

The data on leaf length and the number of leaves of plants with and without spiders were $\log_{10}$ transformed for normalization and homogenization of the variances (Sokal & Rohlf 1995). The data were then compared by repeated measures analyses of covariance (ANCOVA) in a completely randomized design (Hurlbert 1984) in which treatment was a fixed effect, time was the repeated factor, and the initial measure was the covariate (Sokal & Rohlf 1995).

Isotopic analyses

The ^{15}N atom % and $\delta^{15}N = [((^{15}N:^{14}N_{sample}/^{15}N:^{14}N_{standard}) - 1) \times 1000]$ of the bromeliad leaves, spider feces, carcasses, flies and spiders (natural abundances and enriched) were determined using an Elemental Analyzer ANCA-SL (Automatic Nitrogen and Carbon Analyzer) mass spectrometer with a magnetic sector of low resolution, coupled to an IRMS 20-20 (Europe Scientific, Krewe, UK).

To estimate the fraction of plant nitrogen derived from spiders in the field (% $N_{dfspider}$), we used the equation of the simple two-member mixing model:

$$\%N_{dfspider} = \left(\frac{\delta^{15}N_{Bb\,spider} - \delta^{15}N_{Bb\,reference}}{\delta^{15}N_{F} - \delta^{15}N_{Bb\,reference}} \right).100 \tag{1}$$

where $\delta^{15}N_{Bb\ spider,}$ $\delta^{15}N_{Bb\ reference}$, and $\delta^{15}N_F$ are, respectively, the mean $\delta^{15}N$ values for *B. balansae* leaves at high (area 1), intermediate (reference plants, mean value for area 2) and low (reference plants; mean value for area 3) spider densities and for feces (natural abundance). The calculation to determine the fraction of plant N derived from labeled spider feces and carcass was done based on APE (atom % ^{15}N excess), through the following equation:

$$\%N_{dfspider} = \left(\frac{APE_{Bb}}{APE_{feces}} \right).100 \tag{2}$$

where APE_{Bb} ($APE_{Bb} = AP_{Bb} - AP_{control}$) and APE_{feces} ($APE_{fezes} = AP_{fezes} - AP_{control}$) are the mean atom % excess values for *B. balansae* leaves that received labeled feces or carcasses, and for feces respectively. AP is the mean atom % value for each sample. The values of $\delta^{15}N$ for the field-grown bromeliads and spider feces (natural abundance), and of atom % ^{15}N for the labeled bromeliad leaves, feces, carcasses, flies and spiders are given respectively in the Table 1 and 2.

HPLC and other analyses

To determine the N-containing compounds in spider feces, the feces of five adult female spiders were diluted in distilled water (pH 7.5), passed through 0.2 µm filters and analyzed by reversed-phase high performance liquid chromatography (RP-HPLC). The compounds were separated on a C_{18} column (Supelco, 5 µm, 4 mm x 250 mm) using aqueous 0.5 M sodium acetate as the solvent at a flow rate of 0.8 ml/min. The compounds that eluted from the column were monitored with a diode array detector operating at 190-340 nm. Pure hypoxanthine, uric acid, urea, adenine and guanine were used to construct a calibration curve to determine the concentration in the samples.

Samples of soil from near the roots and of green leaves from *B. balansae* growing in the field were tested for the presence of microorganisms with an ability to degrade guanine. Soil (one gram; n=5) and green leaves (n=2) were vigorously shaken in 50 ml of distilled water for 12 h and 0.5 h, respectively. 100 µl aliquots were then spread on minimum solid medium (Sambrook et al. 1989) containing guanine as the only source of carbon and nitrogen. The medium was maintained for 72 h at 30ºC.

RESULTS

The bromeliads from sites with higher spider density presented values of $\delta^{15}N$ more positive compared to bromeliads from sites with intermediate and low spider density (Table 1). Using the equation 1, we calculated that a range of 30-44% of the total nitrogen of bromeliads in the field may have derived from spider feces. Our laboratory manipulations showed that *Drosophila* flies, the spiders that fed on these flies and their feces were strongly ^{15}N-enriched (Table 2). The greenhouse experiment showed that the values of atom % ^{15}N for leaves were higher after treatment with feces (feces > dead flies > carcass >

control; Table 2), indicating that feces were more important than entire dead insects and discarded insect carcasses as a source of plant nitrogen. During this experiment (48 d), we determined through the equation 2 that the spider feces, dead flies and carcass contributed, respectively to 15%, 6% and 3% of the total nitrogen of *B. balansae*. The contrast between the N derived from spiders in the field and in greenhouse may have occurred because the plants in the field had more spiders, which consequently produced more feces, silk and prey remains. In addition, bromeliads in the field had more time in contact with spider debris (>2-3 y) than the bromeliads used in the greenhouse experiment (48 d).

Our field experiment showed that in the presence of spiders new leaves of bromeliads grew 15% longer than those of plants without spiders ($P = 0.023$, Fig. 2A, Table 3). In this experiment, the $\delta^{15}N$ values of leaves from bromeliads with spiders were significantly higher than those bromeliads from which spiders were excluded (Mann-Whitney, $P = 0.006$, Table 1). Using the equation 1, we calculated that spider debris (feces) contributed with 13% of the total N (%) of bromeliads with spiders. The length of the mature leaves and the number of leaves produced by the bromeliads in the absence and presence of spiders did not differ statistically ($P \geq 0.06$, Fig. 2B and C, Table 3). The drop in number of green leaves observed in the spiders absent treatment at sampling date 2 (Fig. 2C) was probably caused by the increase in frequency of older (green) leaves that died; dead leaves were not counted in this experiment.

Using HPLC, we verified that guanine was the most abundant N-containing compound found in the feces of *P. chapoda* (~35 µg/fece), although traces of uric acid and hypoxanthine were also detected. Bacteria obtained from leaves and soil all grew in guanine enriched medium, but were more numerous in the soil. A hundred colonies picked up from the soil samples also grew when replicated onto fresh medium.

DISCUSSION

Our findings strongly support the hypothesis that *B. balansae* can incorporate nutrients excreted by associated predators. In contrast to carnivorous bromeliads (e.g., *Brocchinia reducta*) that produce smells, morphological traits and enzymes to respectively attract, capture and digest insect prey (Givnish et al. 1984, Benzing 2000), *B. balansae* present no obvious adaptive feature to directly obtain animal nutrient. In addition, contrary to many bromeliad rosettes that form phytotelm are therefore considered as saprophytic (Benzing 2000), *B. balansae* does not form phytotelm. On the other hand, this plant has large thorns in the leaf margins and an architecture that provide refuge, foraging and reproductive sites, and nurseries for *P. chapoda*, therefore improving the fidelity of this participant (Romero & Vasconcellos-Neto 2005a,b,c). The spiders promote host plant nutrition via an indirect process: they capture and digest prey analogously to carnivorous plants and concentrate nutrients through their debris inside the rosettes. Therefore, plant nutrition derived from animals can occur even in the absence of carnivorous or saprophytic habits (see Anderson & Midgley 2003). According to Anderson & Midgley (2003), digestive mutualisms (i.e., mutualisms involving animals that contribute with plant nutrition) only substitute digestive organs in plants if they are obligate and host specific (Anderson & Midgley 2003). In fact, the association between *P. chapoda* and *B. balansae* is highly specific and very commom throughout several regions of cerrados (savanna-like vegetation) and semi-deciduous forests from South America (Rossa-Feres et al. 2000, Romero & Vasconcellos-Neto 2005a,b,c, G.Q. Romero, unpublished data).

Although absorptive trichomes are more abundant on the leaves of *B. balansae* than on other terrestrial, root-based bromeliads and can absorb minerals (Benzing & Burt 1970), they are probably unable to incorporate amino acids (Benzing et al. 1976). Since the nitrogen compounds excreted by the spiders (e.g., guanine) are simplest than amino acids, they might be incorporated directly through the trichomes as well as after being mineralized by bacteria (and perhaps other microorganisms) found on the leaves and roots of *B. balansae*. In the notorious mutualisms involving phytotelm bromeliads and associated microorganisms (e.g., bacteria), the saprophytic plants intercept litter and the symbionts decompose and mineralize phytomass, becoming available to plant uptaking (Benzing 2000). Bacteria are also present in insectivorous plants and are probably associated with prey digestion (see Anderson & Midgley 2003). It is possible that bacteria found here may constitute a third component, characterized as a second-order mutualist in this spider-plant system.

Since the soils where *B. balansae* lives (e.g., South American savannas) are typically poor and acidic (Oliveira & Marquis 2002), spider-supplied nitrogen could provide a major benefit to this plant species. Indeed, our field experiment showed that in the presence of spiders new leaves of bromeliads grew longer than those of plants without spiders. Several groups of animals, including other jumping spider species, are strictly associated with bromeliads, where they hide, forage and reproduce (Benzing 2000, Machado & Oliveira 2002, Romero & Vasconcellos-Neto 2004, 2005a, b). These animals can potentially fertilize their host plants with fecal remains and other debris. There are some examples of animals that contribute with plant nutrition (Huxley 1980, Rico-Gray et al. 1989, Treseder et al. 1995, Ellis & Midgley 1996, Sagers et al. 2000, Anderson & Midgley 2003, Fischer et al. 2003, Solano & Dejean 2004). However, to our knowledge, this is the first study to document digestive mutualism in the Bromeliaceae and between spiders and plants, and simultaneously show that animals can improve plant performance by the nutrition through their debris.

Terrestrial bromeliads without phytotelmata, such as *B. balansae*, are assumed to depend on the soil for nutrient acquisition (Benzing 1986, Endres & Mercier 2003) and to be better adapted to absorb and assimilate inorganic nitrogen. In contrast, tank-bromeliads, especially those with epiphytic habits, are better adapted to make use of organic nitrogen (Owen-Jr & Thomson 1988, Endres & Mercier 2001) and are probably more dependent on the vegetation and faunal debris for nutrition (Benzing 1986). We therefore suggest that tank-bromeliads may benefit even more from animal nutrient input.

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Table 1. Mean δ^{15}N values for the leaves of natural-grown (natural abundance) individuals of *B. balansae*, of plants used in the field experiment and of spider feces. The δ^{15}N values for the natural-grown plants were determined for field bromeliads with three levels of spider density (Mean±SE spiders/bromeliad: High = 2.91±0.53; Intermediate: 0.60±0.10; Low: 0.08±0.03). N = number of replicates.

	δ^{15}N ‰ (SE)	N
Natural-grown plants		
Area 1: high spider density	4.83 (0.39)	5
Area 2: intermediate spider	1.67 (0.33)	5
Area 3: low spider density	-0.95 (1.34)	5
Field experiment		
Spiders present	3.21 (0.33)	16
Spiders absent	1.88 (0.34)	16
Feces	12.10 (2.71)	3

Table 2. Mean atom % ^{15}N values for the leaves of greenhouse-grown individuals of *B. balansae* (enriched), and for the enriched (~20% atom % excess) spider feces, *Drosophila melanogaster* carcasses left by spiders, intact *D. melanogaster* flies and adult spiders. Nitrogen uptake was determined in a greenhouse by applying ^{15}N-enriched spider feces (treatment 1), ^{15}N-enriched *Drosophila melanogaster* flies (dead) (treatment 2) and *D. melanogaster* carcasses discarded by spiders after feeding (treatment 3) in two-day intervals over 48 days. N = number of replicates.

	atom % ^{15}N (SE)	N
Greenhouse experiment		
Treatment 1: feces	1.558 (0.084)	5
Treatment 2: dead flies	1.151 (0.168)	5
Treatment 3: carcass	0.684 (0.044)	5
Control	0.370 (0.001)	5
Feces enriched	8.395 (0.598)	4
Carcasses enriched	11.805 (0.657)	4
Drosophila melanogaster		
Unenriched	0.3674 (0.00007)	2
Enriched	13.643 (0.804)	4
Spiders (adult females)		
Unenriched	0.3728	1
Enriched	3.036 (0.628)	4

Table 3. Repeated measures analysis of covariance (ANCOVA) of the field experiment examining the effects of the presence of *Psecas chapoda* spiders on leaf growth and leaf production in *Bromelia balansae*. The first measure (pre-treatment) was used as the covariate.

Source of variation	df	MS	F	P	G-G
Growth of new leaves					
Spider	1	0.081	5.95	0.023	
Pre-treatment	1	0.022	1.63	0.215	
Error	22	0.014			
Time	3	0.045	31.36	<0.001	<0.001
Time x spider	3	0.002	1.35	0.265	0.267
Time x pre-treatment	3	0.034	23.77	<0.001	<0.001
Error	66	0.001			
Growth of mature leaves					
Spider	1	0.010	3.93	0.058	
Pre-treatment	1	0.141	56.77	<0.001	
Error	27	0.002			
Time	2	0.002	4.47	0.016	0.033
Time x spider	2	0.000	0.41	0.670	0.579
Time x pre-treatment	2	0.002	4.15	0.021	0.040
Error	54	0.000			
No. of green leaves					
Spider	1	0.013	2.72	0.111	
Pre-treatment	1	0.124	25.53	<0.001	
Error	27	0.005			
Time	3	0.003	3.86	0.018	0.012
Time x spider	3	0.003	3.09	0.040	0.031
Time x pre-treatment	3	0.003	3.17	0.037	0.029
Error	81	0.001			

Figure caption

Fig. 1. Adult female jumping spider (*Psecas chapoda*) inside its eggsac on the concave surface of a *Bromelia balansae* leaf. Scale bar: ~1 cm. Photo credit: Gustavo Q. Romero.

Fig. 2. Field experiment showing (A) the growth of new leaves, (B) of mature leaves, and (C) leaf production in *Bromelia balansae* in the absence (open circles) and presence (filled circles) of jumping spiders. Sampling dates: 1 = May 10, 2003; 2 = Aug 1, 2003; 3 = Nov 4, 2003; 4 = Feb 10, 2004; 5 = May 1, 2004.

Fig. 1

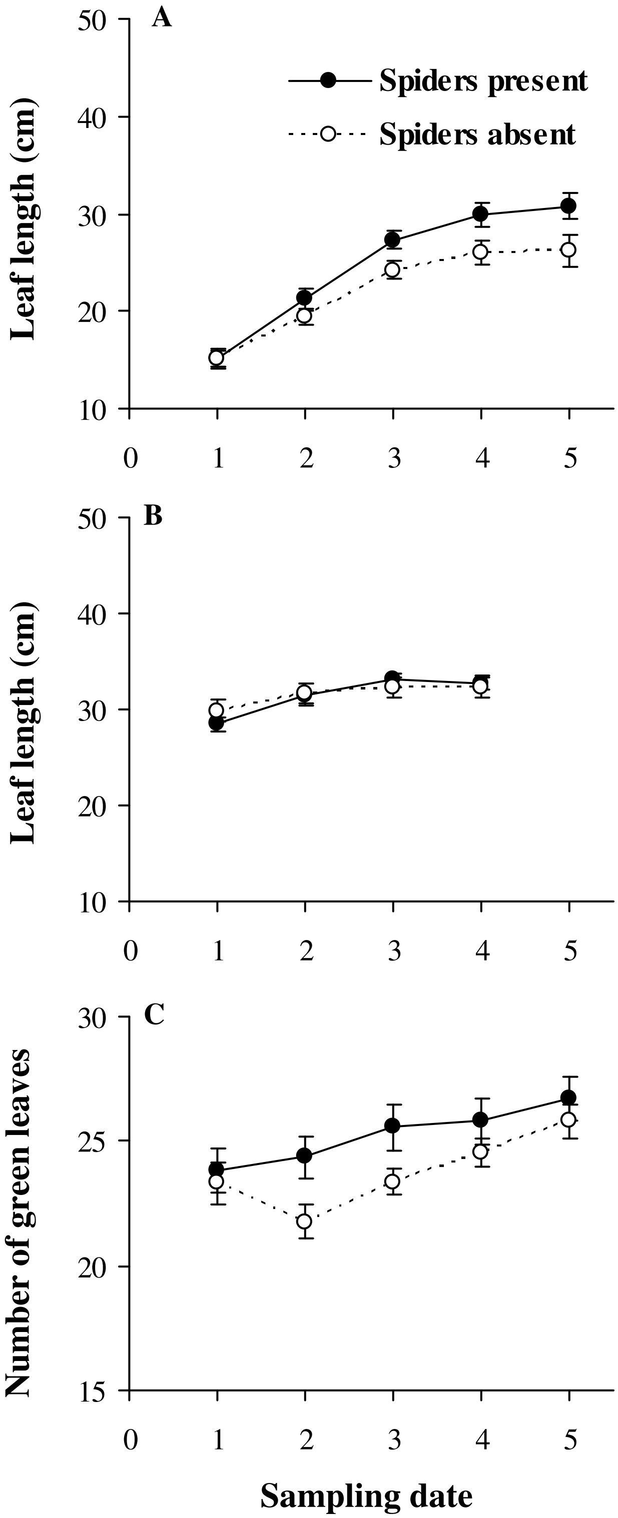
A
B
C
Spiders present
Spiders absent
Leaf length (cm)
Leaf length (cm)
Number of green leaves
50
40
30
20
10
30
25
20
15
0
1
2
3
4
5
Sampling date

Fig. 2.

Artigo 8

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Spatial variation in the strength of the mutualism between a jumping spider and a terrestrial bromeliad

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Abstract

Psecas chapoda, a neotropical jumping spider strictly associated with the terrestrial bromeliad *Bromelia balansae* in cerrados and semi-deciduous forests from South America, effectively contributes to plant nutrition and growth. In this study we investigated if the strength of this spider-plant mutualism differs spatially with varying spider densities. Using stable isotope methods, we found a positive significant relationship between spider density among forest fragments and δ^{15}N values for bromeliad leaves. Spider debris contributed to 30-40% of the total N of *B. balansae* in sites with high spider density, and to 7-31% in sites with low to intermediate spider density. Bromeliads from open grasslands were associated with spiders and presented higher values of δ^{15}N compared to forest bromeliads, which maintain no association with spiders. Despite this, forest bromeliads presented higher total N concentrations than bromeliad from grasslands. These results suggest that the bromeliad nutrition is more litter based inside forests and more spider based in open grasslands. This is one of few studies to show nutrient provisioning and conditionality in a spider-plant system.

Keywords Mutualism · Conditional outcomes · Spider-plant relationships · Stable isotope ^{15}N

Introduction

Mutualisms are inter-specific interactions in which the partners experience a net benefit. Classical examples of mutualism between animals and plants come from interactions between flowering plants and pollinators or seed dispersers (Faegry & van der Pijl 1979, Jordano 2000), ants and extrafloral nectaried plants or myrmecophytes (reviewed in Heil & McKey 2003), mites and leaf domatia (reviewed in Romero & Benson 2005), figs and fig wasps (Weiblen 2002, Cook & Rasplus 2003), and yucca and yucca moths (Addicott 1998, Pellmyr & Krenn 2002). The origins, as well as the mechanisms responsible for persistence and breakdown of these mutualisms are generally evaluated in perspectives of costs and benefits (Boucher et al. 1982, Bronstein 1994, 2001). Variation in the balance of costs and benefits of an association may arise from many causes (Thompson 1988), including conditional outcome, a phenomenon that describes how mutualism varies in space and time (Bronstein 1994, Herre et al. 1999).

Although spiders are among the most common predators on plants, frequently involved in complex terrestrial food webs (Riechert & Bishop 1990, Spiller & Schoener 1994, Polis & Hurd 1995) or in direct and indirect interactions with other arthropods and host plants (Schmitz 1998, Gastreich 1999, Schmitz & Suttle 2001, Romero & Vasconcellos-Neto 2004), little is know about mutualistic interactions between spiders and plants (Whitney 2004), especially if the spiders contribute to plant nutrition through nutrient provisioning (digestive mutualism) (Romero et al. 2005).

The neotropical jumping spider *Psecas chapoda* (Peckham & Peckham) (Salticidae) has a host-specific distribution, inhabiting obligately *Bromelia balansae* Mez. (Bromeliaceae) in several regions of Brazil, Bolivia and Paraguay (Höfer & Brescovit 1994, Rossa-Feres *et al*. 2000, Romero & Vasconcellos-Neto 2005 a, b, c, G. Q. Romero 2005). In this unusual association, the spiders obtain foraging, mating and laying egg sites, shelter for adults and immatures and nurseries for spiderlings (Rossa-Feres *et al*. 2000, Romero & Vasconcellos-Neto 2005 a, b, c). Consequently, they contribute to *B. balansae* nutrition and improve plant growth (Romero et al. 2005). However, factors negatively affecting the spider density could disrupt this spider-plant mutualism and the net benefit to *B. balansae*. For instance, Romero & Vasconcellos-Neto (2005c) reported that *P. chapoda* does not occur inside forests because dry leaves fallen from trees block the rosette base used as shelter. Here we used isotopic methods to investigate if (1) the strenght of this spider-bromeliad mutualism varies spatially with varying spider densities, and (2) bromeliads living in sites with low spider density are nutritiously depleted.

Material and methods

Study area and organisms

The study was done in semi-deciduous tropical forests surrounded by open grassland areas, in the region of Dois Córregos city (22º21'S, 48º22'W), São Paulo state, southeastern Brazil, from May 2003 to December 2004. The climate consists of a distinct dry/cold (May-September) and wet/warm (October-April) season with a mean annual rainfall of 1600 mm (Romero & Vasconcellos-Neto 2005 c). The soil is sandy, acidic and poor in nutrients (see Table 1).

Bromelia balansae (Bromelioideae) is a large (>1 m tall) spindly-leaved, terrestrial bromeliad very conspicuous for acidic, nutrient poor cerrado (savanna-like vegetation) and semi-deciduous forests from South America (Romero 2005). Its leaves are concave with thorny margins, and do not form a tank to store water, but may retain a few milliliters of rainwater which would allow for extended periods of nutrient dissolution and uptake by the plant leaves (Romero et al. 2005). This semelparous bromeliad blooms in the beginning of the rainy season (October-November) (Rossa-Feres *et al*. 2000, Romero & Vasconcellos-

Neto 2005 b) and produces a central inflorescence with pink-lilac flowers that are frequently visited by hummingbirds (G.Q. Romero, personal observation). In the study area, *B. balansae* typically occurs inside forests (understorey) and in open grasslands, up to 30 m from the forest margins, and present similar density between these two habitats (Romero & Vasconcellos-Neto 2005 a).

Psecas chapoda spends its entire life cycle, including courtship, mating, egg sac formation, molting, and population recruitment on this plant (Rossa-Feres et al. 2000, Romero & Vasconcellos-Neto 2005 b). In patches with high spider density, 90-100% of the bromeliads are typically occupied by *P. chapoda* over the year, and a unique individual of *B. balansae* can shelter up to 22 adult and immature spiders (Romero & Vasconcellos-Neto 2005 a, b). These spiders prey on a great variety of insects and other web and jumping spiders (G.Q. Romero, unpublished data). Since the spiders generally remain on the concave, upper side of the leaves (G. Q. Romero, personal observation), and adult females produce several egg sacs in this region throughout the year (Rossa-Feres *et al*. 2000, Romero & Vasconcellos-Neto 2005 a, b), feces, silk from egg sacs, prey remains and exuviae are trickled to the base of the plant rosette, where can be absorbed by the roots and/or leaves (Romero et al. 2005).

Spatial variation in the spider-plant relationship

Since *P. chapoda* contributes to *B. balansae* nutrition (Romero et al. 2005), bromeliads living in sites with high spider density could present larger amount of nitrogen derived from spiders (i.e., isotope ^{15}N) in their leaf tissues than bromeliads from sites with spider absent or in low density. In addition, bromeliads could be nutritiously depleted (total N concentration) in sites/habitats with low spider density (e.g., forest understorey, see Romero & Vasconcellos-Neto 2005 c). These hypotheses were tested using isotopic methods to quantify the natural abundance of the stable isotope ^{15}N present on leaves of *B. balansae* in sites of varying spider density. For this, we used three forest fragments (~ 0.3-4.0 ha in size) surrounded by a matrix of open grassland, and two isolated patches (thickets) of *B. balansae*, one in open grassland (n=21 bromeliads) and other inside a forest (n~40 bromeliads). We used only fragments close from each other to avoid spatial variation in soil properties (e.g., nutrient concentration, pH etc.). Each site (forest fragment and patch) distanced from its neighbours in ~ 0.1-1.0 km.

The number of spiders and egg sacs per bromeliad was estimated in each habitat (forest and grassland) of each site by inspecting the first 10-22 bromeliads in two parallel 50 m x 20 m transects (20-30 m apart), one in open grassland and other inside forest. In the patches, we estimated the number of spiders and egg sacs by inspecting the first 10-14 bromeliads from open grassland area and 9-12 bromeliads from forest. The number of spiders and egg sacs per bromeliad was determined four times, two in the dry season (June 19, August 28, 2004), and two in the rainy season (October 11, December 4, 2004). However, only mean values of spider density per site and habitat were used in the analyses.

In each site, we collected two new leaves (second layer) of five bromeliads. The bromeliads were in vegetative phase, and had similar age (~ 3-4 y). After survey, each leaf was washed for at least 3 min in current water and scrub by hand to eliminate contamination (organic particles or mites). Bromeliad leaves were oven-dried for 30 h at 65ºC, ground to a fine powder in ball mill, and transferred to airtight containers for δ^{15}N (‰) and N concentration (g/Kg) determinations.

For each site and habitat, we collected five samples of soil close to the bromeliads (up to 40 cm apart), at ~10 cm below ground, to determine soil N concentration and pH for comparative analyses. Accumulated leaf litter collected of three bromeliads from each forest site were dried and homogenized for $\delta^{15}N$ (‰) and N concentration (%) determinations. Three to five adult females of *P. chapoda* per open grassland area were collected and maintained in pots for 4-6 d, and their feces were diluted in distilled water, homogenized, and then dried in Savant Speed Vac Concentrator System to determine their $\delta^{15}N$ and total N values. One individual of *P. chapoda* and silk from three egg sacs (from open grassland, site 1) were frozen and lyophilized to determine their $\delta^{15}N$ values.

To test for the relationship between spider and egg sac density and $\delta^{15}N$ values in the leaf tissues of the bromeliads, we used linear regressions after $\log_{10}$ transformation of the values of spider and egg sac density (Sokal & Rohlf 1995). We compared the $\delta^{15}N$ and N concentration between habitats (grassland and forest) using randomized block ANOVA, in which habitat was a fixed effect and block (fragment or patch) was the random effect. Since some patches (S4Gr and S5Fo) were not paired, these analyses were run considering missing values. Prior to the tests, the data on N concentration and $\delta^{15}N$ were $\log_{10}$ transformed to homogenize the variances and to meet the assumption of normality. A value of 5 was added to all values of $\delta^{15}N$ to allow for transformation of negative numbers (reaching -4.02) and zeros.

Contribution of spiders to bromeliad nutrition

To determine the fraction of nitrogen ($\% \, N_{dfspider}$) that grassland bromeliads gain from *P. chapoda* feces and silk from eggsacs in sites with varying spider density, we used the equation of isotopic dilution:

$$\%N_{dfspider} = \left(\frac{\delta^{15}N_{with\ spiders} - \delta^{15}N_{reference}}{\delta^{15}N_{feces\ or\ silk} - \delta^{15}N_{reference}} \right) .100 \qquad (1)$$

where $\delta^{15}N_{\text{with spiders}}$ = mean isotopic nitrogen values for leaves of *B. balansae* from each site/habitat with spiders (density: 0.6-3.0 spiders/bromeliad), $\delta^{15}N_{\text{reference}}$ = mean isotopic nitrogen values for leaves of *B. balansae* from all sites/habitats without spiders or with spiders in very low density (<0.45 spiders/bromeliad; forest bromeliads), and $\delta^{15}N_{\text{feces or silk}}$ = isotopic nitrogen values for feces from each site/habitat (Table 1) or silk from *P. chapoda* egg sacs. To improve the reliability of spider contribution, we used additional reference plants (mean $\delta^{15}N$=1.88‰, n=16) that consisted of potted *B. balansae* from a grassland open area (S1Gr), with age (~ 3.5 y) similar to the natural-growing plants, used as a control in a spider exclusion experiment (Romero et al. 2005). Because isotopic values for spider feces were similar among sites (Table 1), we assume that any organic material from spiders will be similar among sites. We therefore used mean value for silk of three egg sacs ($\delta^{15}N$=24.5 ‰ ± 2.85 SE) from only the site with high spider density (see S1Gr in Fig. 1).

Nitrogen analyses

The $\delta^{15}N$, defined by $[(^{15}N: {}^{14}N_{sample}/{}^{15}N: {}^{14}N_{standard}) - 1] \times 1000$, and N concentration from leaves, feces, silk of eggsacs and litter were determined using an Elemental Analyzer ANCA-SL (Automatic Nitrogen and Carbon Analyzer) mass spectrometer with magnetic sector of low resolution, coupled to an IRMS 20-20 (Europe Scientific, Krewe, UK). Three to five determinations of $\delta^{15}N$ (‰) and N concentration (g/Kg) for each sample (bromeliad leaves and litter) were performed in order to minimise sampling errors, but only the mean value for each sample was analysed and/or presented. The soil N concentration was determined by the Kjeldahl method, and soil pH was determined by the $CaCl_2$ method (Binkley & Vitousek 1989). Values of soil N concentration and soil pH were similar among sites and between habitats (open areas and forests) (Table 1). Delta ^{15}N values for feces were also similar among the open grassland areas (Table 1).

Results

There was a significant positive relationship between spider density among sites/habitats and mean $\delta^{15}N$ values for bromeliad leaves ($r^2 = 0.92$, $P < 0.001$, Fig. 1A). While in the grassland the relationship between spider density and $\delta^{15}N$ values for leaves was significant ($r^2 = 0.96$, $P = 0.022$), our regression analysis did not detect this relationship inside the forest ($r^2 = 0.80$, $P = 0.103$). Similarly, the density of egg sacs was also correlated with $\delta^{15}N$ values for bromeliad leaves among sites/habitats ($r^2 = 0.76$, $P = 0.005$, Fig. 1B).

However, the relationship between egg sac density and δ^{15}N values for leaves was not significant in grassland ($r^2 = 0.80$, P = 0.106) as well as inside forest ($r^2 = 0.87$, P = 0.070). While the highest δ^{15}N value for bromeliad leaves (δ^{15}N = 4.83 ‰) was found at the area with high spider and egg sac density, the lowest δ^{15}N values for leaves (δ^{15}N = -0.95 to 0.018‰) were found in the areas with spiders and egg sacs absent or in very low density (S1Fo, S3Fo, S5Fo, Fig. 1). Since faecal δ^{15}N values were similar among open grassland areas, and soil N concentration was similar among sites and habitats (Table 1), we attribute that this variation in leaf δ^{15}N values was, in fact, caused by the variations in spider density among sites/habitats.

Using the EQ. 1, we calculated that a range of 30-40% of the total nitrogen ($\%N_{Bb}$) of *B. balansae* was derived from spider feces in the area with highest spider density (S1Gr). In sites with intermediate (S2Gr) and low spider density (S3Gr and S4Gr), spiders contributed respectively to a range of 17-31% and 0-22% of the total nitrogen of bromeliads. If *B. balansae* was able to absorb nitrogen from spider silk, the percentage of nitrogen of bromeliads derived from silk was 13-20% in the site with highest spider density, 8-15% in the site with intermediate spider density, and 0-11% in the sites with low spider density.

Bromeliads from open grassland areas had higher values of δ^{15}N than bromeliads from forest undergrowths (*P*<0.001, Table 2). In contrast, forest bromeliads had higher N concentration than grassland bromeliads (*P*=0.028, Table 2), as shown in Fig. 2. The values of fecal δ^{15}N were 3-6 times higher than the values of leaf litter δ^{15}N (Table 1).

Discussion

Our findings show that the benefit to *Bromelia balansae* varied depending on the density of the spiders among environments and sites: bromeliads from sites with higher spider density presented higher values of $\delta^{15}N$ than bromeliads from sites where spiders were rare or absent. This spatial conditional outcome occurred in part because *Psecas chapoda* were infrequent on forest-dwelling bromeliads. Dry leaves falling from forest trees block the internal base of the bromeliad rosettes, probably reducing the availability of shelter for adult spiders and entirely eliminating the nurseries for the spiderlings (Romero & Vasconcellos-Neto 2005 a, c). This environment dependent mutualism may extend to a geographic scale, since all populations of *P. chapoda* were found on grassland-dwelling *B. balansae* in several regions of Brazil, Paraguay and Bolivia (Romero 2005). The factors causing variation in spider density among open sites were not completely clear, but prey availability may explain this pattern of spider distribution. In at least one area (S1Gr), the high spider density was possibly related to the proximity of a water source, which provides alloctonous, extra prey (e.g., chironomids) for spider population over the year (Romero & Vasconcellos-Neto 2005 b, c). Romero & Vasconcellos-Neto (2005c) showed experimentally that prey availability, besides of dry leaves fallen from trees, may affect the spatial distribution in *P. chapoda*. Temporal and spatial conditional outcomes have been documented for protective mutualism in some spider-plant systems (Romero & Vasconcellos-Neto 2004, Whitney 2004). However, this is the first study showing spatial conditionality in a digestive mutualism (Anderson & Midgley 2003) between spiders and plants. These variable outcomes are key to understanding the ecological and evolutionary trajectories of facultative mutualisms (Bronstein 1994, Thompson 1999, Whitney 2004).

The amount of nitrogen in *B. balansae* derived from spiders in sites with high spider density (30-40%) is comparable to the nitrogen acquisition from prey in carnivorous plants. Generally, carnivorous plants (e.g., *Drosera*, *Roridula*, *Nepenthes* and *Darlingtonia*) derive large amounts of nitrogen (50% to 76%) from arthropods (Dixon et al. 1980, Schulze et al. 1991, 1997, Anderson & Midgley 2002). However, arthropod nitrogen in *B. balansae* exceeded arthropod nitrogen in the pitcher plant *Cephalotus follicularis* (26%) (Schulze et al. 1997), even in sites with intermediate spider density (17-30%). Members of the Bromeliaceae have their leaves organized in a rosette shape, able to intercept and retain water and organic matter. In addition, their leaves have absorptive trichomes that uptake water and nutrients. The density of absorptive trichomes on leaves of *B. balansae* is higher than on leaves of other terrestrial, root-based bromeliads (Benzing & Burt 1970, Benzing et al. 1976), and might directly absorb nitrogen derived from spiders (e.g., guanine). Alternatively, Romero et al. (2005) found associated bacteria on the leaves and roots of *B. balansae*, which may operate in the mineralization of the nitrogen-rich molecules (e.g., guanine, silk) produced by the spiders.

Individuals of *B. balansae* living in forest understories were depleted in δ^{15}N possibly because the absence of spiders in this habitat. However, these bromeliads presented higher nitrogen concentration in their leaf tissues than bromeliads from open grasslands. Since δ^{15}N values for leaf litter accumulated inside the rosettes from forest bromeliads were 3-6 times lower than δ^{15}N values for spider feces, we suggest that forest bromeliads uptake nitrogen from decomposed litter, while a portion of the nitrogen of grassland bromeliads (13-40%) was probably derived from spider debris. In addition to total nitrogen content, forest bromeliads were larger (Romero & Vasconcellos-Neto 2005 a) and had thinner leaves that apparently contained more chlorophyll (dark green) than those of the exposed plants (weak green to yellowish) (G. Q. Romero, personal observations). Another bromeliad species of this genus (*B. humilis*) that grows in seasonally arid savannas from Venezuela presented similar morphological traits with *B. balansae* when in shaded and exposed habitats, and was considered to be apparently better adapted to partly shaded habitats (reviewed in Martin 1994). Exposed forms of *B. humilis* were often photoinhibited and hence grew more slowly than the plants in the shade (reviewed in Martin 1994). However, when exposed forms were treated with nitrogen, photosynthetic capacity was improved (measured as O_2 exchange) (Fetene et al. 1990). Fetene et al. (1990) suggested that *B. humilis* can fully utilize a high light environment only in the presence of adequate amounts of nitrogen. Possibly, *B. balansae* behaves like *B. humilis* in its photosynthetic capacity in the presence/absence of nitrogen. In a field experiment, Romero et al. (2005) showed that plants of *B. balansae* colonized by *P. chapoda* in open areas grew 15% more than bromeliads in which spiders were excluded. Since the acidic soils from South American savannas are nitrogen deficient (Oliveira & Marquis 2002), spider-derived nitrogen might provide a large benefit to *B. balansae* by improving photosynthetic capacity and increasing plant tolerance in habitats exposed to sunlight.

Although the beneficial effect of *P. chapoda* to *B. balansae* was variable among sites, even at low densities the spider may contribute to plant nutrition (up to 22%). Moreover, the spiders inhabit and reproduce on *B. balansae* over the year (Romero & Vasconcellos-Neto 2005 b), suggesting that this spider-plant mutualism is temporally predictable. In addition, we have found *P. chapoda* to be present in several *B. balansae* populations, through several South American regions (Romero 2005). Since this spider-plant system apparently present no cost to neither partner, this association may be stable, and may persist and evolve throughout their large geographic range.

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Table 1. Characteristics of soil N concentration (%), soil pH, fecal $\delta^{15}N$ (‰) of spiders, and leaf litter $\delta^{15}N$ (‰) and N concentration (%) among sites (fragments and patches) and habitats. Values indicate mean ± 1 SE.

	Sites/habitats							
	Site 1		Site 2		Site 3		Site 4	Site 5
Parameters	Grassland	Forest	Grassland	Forest	Grassland	Forest	Grassland	Forest
Soil N concentration (%)*	0.08±0.01	0.07±0.02	0.09±0.003	0.09±0.002	0.09±0.00	0.11±0.01	0.09±0.01	0.12±0.08
Soil pH	4.43±0.28	4.25±0.29	4.23±0.14	4.27±0.19	4.04±0.04	3.80±0.05	4.34±0.11	4.13±0.21
Fecal $\delta^{15}N$ (‰)	12.10	--	11.65	--	13.00	--	11.32	--
Leaf litter $\delta^{15}N$ (‰)	--	3.13	--	3.54	--	2.17	--	1.89
Leaf litter N concentration (%) **	--	2.25	--	1.82	--	1.78	--	1.6

* Determined by the Kjerdahl method

** Determined by the IRMS method

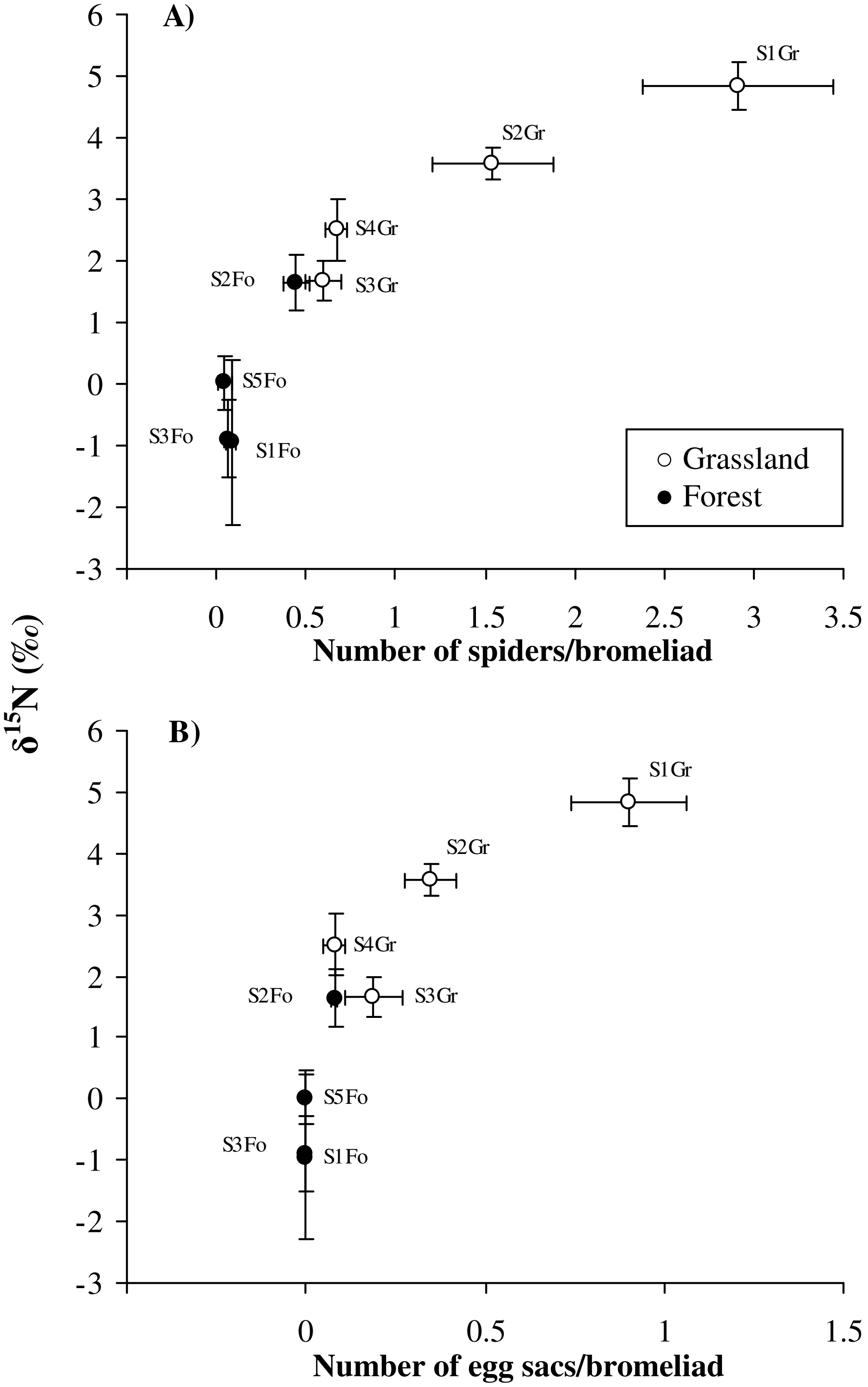
Table 2. Randomized block ANOVA comparing the δ^{15}N and N concentration values for leaves of *Bromelia balansae* living inside forest and open grassland habitats (factor habitat), among sites (fragments or patches; block).

Source of variation	df	*MS*	*F*	*P*
δ^{15}N (‰)				
Habitat	1	0.608	20.59	<0.001
Site (block)	4	0.046	1.55	0.210
Error	34	0.030		
N concentration (g/kg)				
Habitat	1	0.048	5.27	0.028
Site (block)	4	0.041	4.59	0.005
Error	34	0.009		

Figure captions

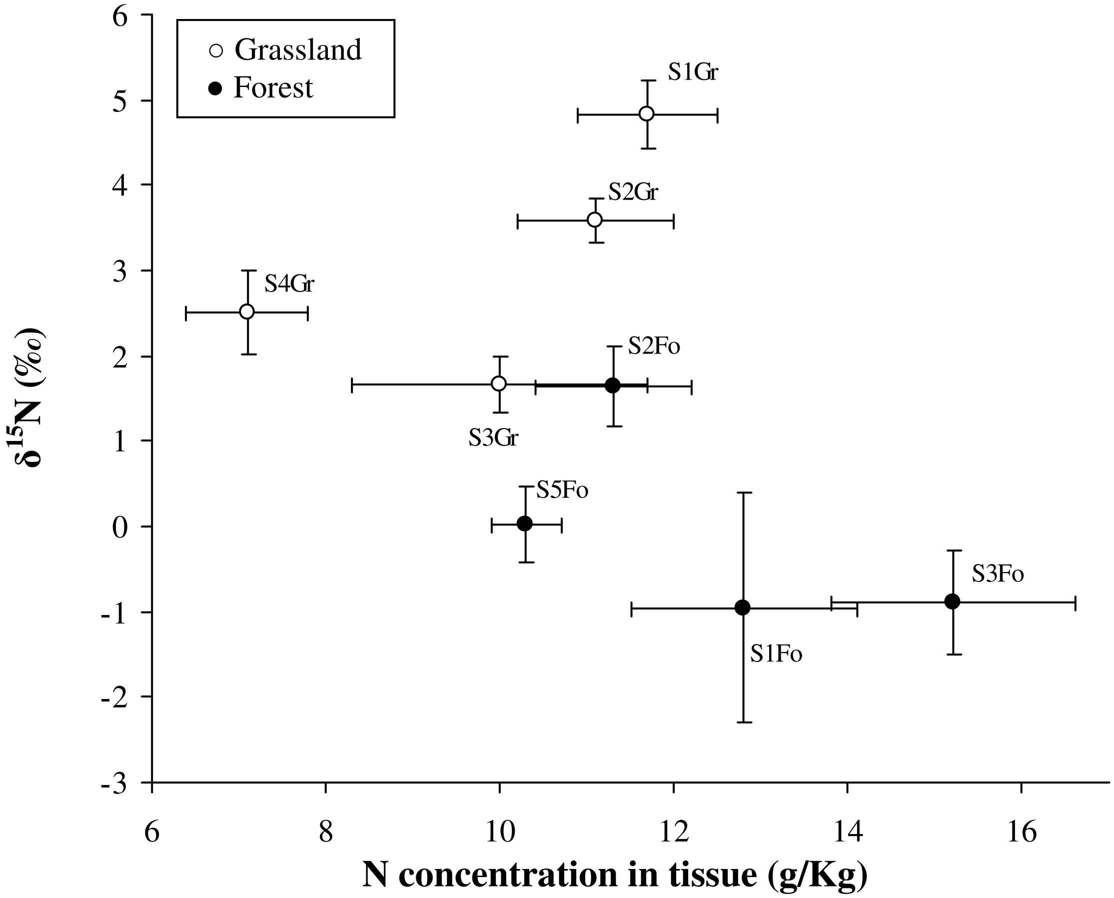
Figure 1. Relationships between density of (A) spiders and (B) egg sacs and foliar $\delta^{15}N$ (‰) values for plants of *Bromelia balansae* growing in different sites (fragments and patches), in open grassland areas (open circles) and inside forests (filled circles). Points represent means and bars represent 1 SE. S=Site, Gr=grassland, Fo=forest. Sites 1-3 represent forest fragments, and sites 4 and 5 represent patches from open area and forest, respectively.

Figure 2. Comparisons of foliar $\delta^{15}N$ (‰) and N concentration (g/Kg) for plants of *Bromelia balansae* growing in different fragments and patches, in open grassland areas (open circles) and inside forests (filled circles). Points represent means and bars represent 1 SE. S=Site, Gr=grassland, Fo=forest. Sites 1-3 represent forest fragments, and sites 4 and 5 represent patches from open area and forest, respectively.



A)
B)
δ15N (‰)
Number of spiders/bromeliad
Number of egg sacs/bromeliad
S1Gr
S2Gr
S3Gr
S4Gr
S1Fo
S2Fo
S3Fo
S5Fo
○ Grassland
● Forest
6
5
4
3
2
1
0
-1
-2
-3
0
0.5
1
1.5
2
2.5
3
3.5

Fig. 1



○ Grassland
● Forest
S1Gr
S2Gr
S4Gr
S2Fo
S3Gr
S5Fo
S3Fo
S1Fo
6
5
4
3
2
1
0
-1
-2
-3
6
8
10
12
14
16
$\delta^{15}N$ (‰)
N concentration in tissue (g/Kg)

Fig. 2

4. SÍNTESE

1. Associações específicas, distribuição espacial e história natural

No presente estudo, dez espécies de aranhas da família Salticidae foram encontradas fortemente associadas a Bromeliaceae, em diferentes fitofisionomias de diversas regiões da América do Sul. Enquanto algumas espécies foram tipicamente especialistas, habitando quase exclusivamente uma espécie de planta em uma extensa área geográfica (e.g., *Psecas chapoda* em *Bromelia balansae*), outras foram generalistas e ocorreram em até 7-8 espécies de bromélias (e.g., *P. sumptuosus*, *Eustiromastix nativo* e *Coryphasia* sp. 1). A disponibilidade regional de espécies de bromélias pode em parte explicar este padrão de uso das plantas hospedeiras. Bromélias são quase exclusivamente da região Neotropical. Suas folhas formam uma arquitetura tridimensional complexa (roseta), que pode ser usada por adultos e imaturos como abrigo contra predadores ou condições climáticas severas, como sítios de forrageamento, acasalamento e de oviposição, e como berçários para as recém emergidas das ootecas. Os salticídeos têm aparentemente evoluído adaptações para explorar este microhabitat distinto e abundante na América do Sul. Espécies de Salticidae de vários gêneros são associadas a bromélias, sugerindo que esta especialização evoluiu várias vezes independentemente.

Em geral, as aranhas Salticidae habitaram e selecionaram as bromélias maiores e/ou aquelas que aparentemente lhes oferecem abrigo contra predadores (e.g., presença de espinhos nas margens das folhas). *Psecas chapoda*, em especial, selecionou ativamente plantas com traços morfológicos distintos, i.e., plantas em fase vegetativa (ausência de inflorescência) e sem folhas secas no centro da roseta. Estes resultados indicam que tais salticídeos bromelícolas podem avaliar, em detalhes finos, o estado físico do seu microhabitat.

Mais espécies de aranhas foram encontradas sobre bromélias de áreas abertas em relação às bromélias do interior das florestas. Estudos desenvolvidos aqui demonstraram que folhas secas que caem das árvores podem bloquear a base central das bromélias, usada pelas aranhas como sítios de refúgios e descanso.

2. Mutualismos

Bromélias têm arquitetura em forma de roseta, que fornece refúgios, sítios de forrageamento e de acasalamento e berçários para os imaturos, portanto aumentando a fidelidade dos seus participantes. Em retorno, tais aranhas promovem a nutrição das bromélias. Usando métodos isotópicos (^{15}N), demonstramos que a aranha *P. chapoda* contribuiu com até 40% do N total de *B. balansae* no campo.

Nutrientes derivados das aranhas poderiam suprir as bromélias que crescem em solos pobres e ácidos comuns na América do Sul. De fato, em um experimento de campo de um ano, plantas com aranhas cresceram 15% mais do que plantas das quais as aranhas foram excluídas. Este é o primeiro estudo a documentar mutualismo digestivo (ou nutricional) em Bromeliaceae e o primeiro a reportar mutualismo desta natureza entre aranhas e plantas. Além disso, este é o primeiro estudo a mostrar que animais podem aumentar a performance das suas plantas hospedeiras através da nutrição.

Presume-se que bromélias terrestres sem fitotelmata, tal como *B. balansae*, dependem do solo para aquisição de nutrientes e são mais bem adaptadas a absorver e assimilar nitrogênio inorgânico. Em contraste, bromélias-tanque, especialmente aquelas com hábito epifítico, são melhores adaptadas a usar nitrogênio orgânico e são mais dependentes da vegetação e fauna para nutrição. Portanto, sugerimos que bromélias-tanque podem se beneficiar ainda mais com a presença de animais. Uma vez que muitas espécies de animais, incluindo várias espécies de aranhas Salticidae, vivem estritamente associadas a bromélias (com presença e ausência de tanque), este tipo de mutualismo envolvendo Bromeliaceae pode ser bastante comum nas regiões neotropicais.

Como muitos sistemas mutualísticos, o mutualismo entre *Psecas* e *Bromelia* foi espacialmente condicional, i.e., aranhas contribuem mais para a nutrição das bromélias onde ocorrem em maior abundância. Bromélias de áreas abertas mantiveram associação com as aranhas e apresentaram valores altos de $\delta^{15}N$ se comparados com os das bromélias das florestas, sem associações com aranhas. Apesar disso, bromélias das florestas tiveram valores maiores de concentração total de N do que bromélias de áreas abertas. Estes resultados sugerem que a nutrição das bromélias é baseada em liteira nas florestas e em detritos de aranhas nas áreas de campos.