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Funções e variabilidade estrutural dos estabilimentos construídos por *Cyclosa fililineata* Hingston 1932 e *Cyclosa morretes* Levi 1999 (Araneae: Araneidae)

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Este exemplar corresponde à redação final da tese defendida pelo(a) candidato (a) Marcelo de Oliveira Gonzaga
e aprovada pela Comissão Julgadora.

João Vasconcellos Neto

Tese apresentada ao Instituto de Biologia da Universidade Estadual de Campinas para a obtenção do título de Doutor em Ecologia.

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"But let thy spiders, that suck up thy venom,
And heavy-gaited toads, lie in their way."

William Shakespeare, *King Richard II*, II, III, ii

"With spiders I had friendship made,
And watch'd them in their sullen trade."

Byron, *The Prisioner of Chillon*

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RESUMO

Aranhas são atacadas por uma grande variedade de inimigos naturais. A pressão de predação e/ou parasitismo pode ter influenciado inúmeras características comportamentais, como a permanência em abrigos construídos na periferia das teias orbiculares e a construção de barreiras de fios. Assim como estas estruturas, os estabilimentos adicionados às teias orbiculares de várias espécies das famílias Araneidae, Tetragnathidae e Uloboridae podem constituir componentes de defesa. As possíveis funções destas decorações compostas por seda e/ou detritos, entretanto, vem sendo intensivamente discutidas deste sua descrição, no final do século XIX. Atração de presas, proteção contra a exposição ao sol, estabilidade, diminuição de danos às teias foram algumas outras funções já atribuídas aos estabilimentos. Neste trabalho apresentamos uma revisão sobre predadores e parasitas de aranhas e sobre as estratégias de defesa utilizadas para minimizar seu sucesso. Em seguida analisamos as presas coletadas por espécies de vespas-caçadoras em duas áreas de Mata Atlântica do sudeste brasileiro, comparando estes dados com a disponibilidade de aranhas no campo. A composição em espécies de aranhas orbitelas e o tamanho das presas capturadas pelas vespas indicaram que a seleção de presas não está baseada apenas na abundância relativa de espécies de aranhas e em seus tamanhos. Aranhas construtoras de estabilimentos, por exemplo, foram capturadas com uma freqüência bem menor que a esperada, sugerindo que essas estruturas podem evitar a predação por vespas. No capítulo seguinte são apresentados dados referentes a variabilidade estrutural dos estabilimentos construídos por *Cyclosa fililineata* e *Cyclosa morretes*. Colunas de detritos são mais freqüentes nas duas espécies, mas estruturas descontínuas são relativamente comuns em teias de imaturos e machos de *C. morretes*. Este tipo, assim como estruturas compostas por seda (espiral e linear) constituem estágios de transição na construção de

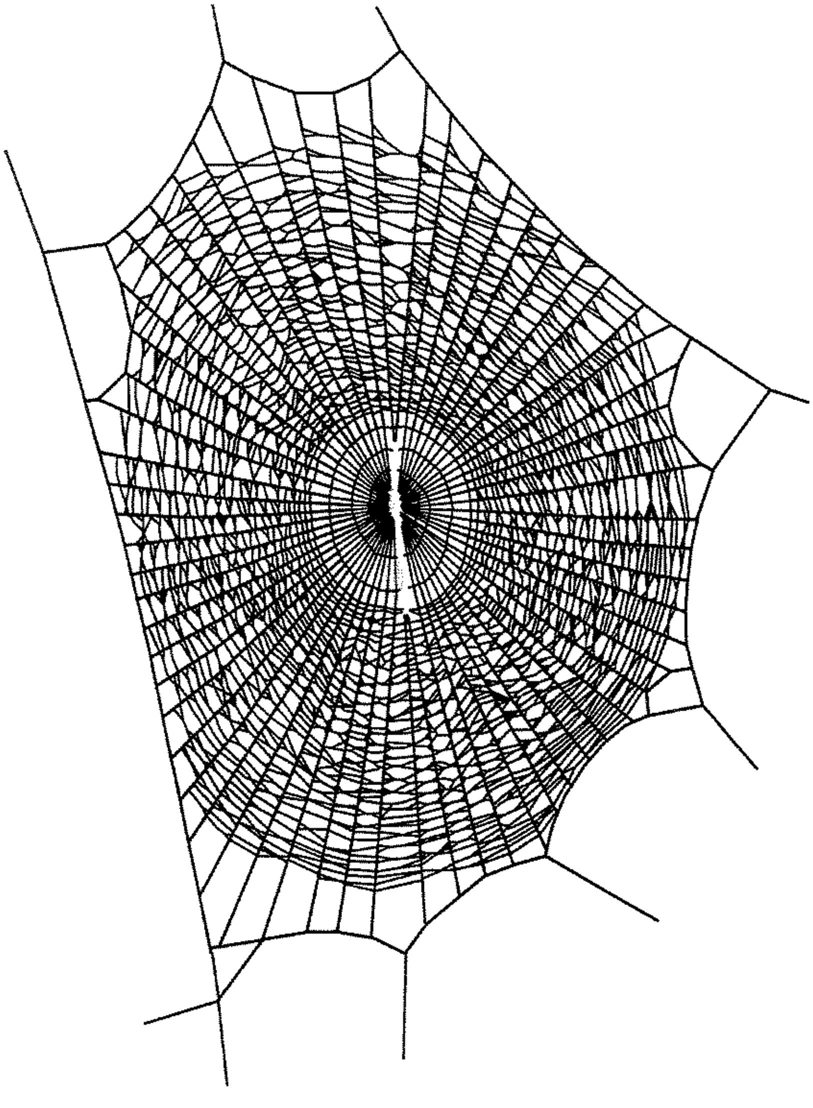
estruturas contínuas. Observamos também uma grande variação na posição ocupada pelas aranhas na coluna de detritos, o que pode reduzir ainda mais a eficiência de ataques por predadores visualmente orientados. Em seguida apresentamos um trabalho testando as duas principais hipóteses sobre as funções dos estabilimentos, defesa contra predação e atração de presas. Os resultados obtidos sugerem que as estruturas de detritos de *C. morretes* e *C. fililineata* não atraem presas, mas podem reduzir a freqüência de ataques por possíveis predadores. No último capítulo investigamos a ocorrência de parasitismo em jovens e adultos, por ichneumonídeos, e em ootecas, por parasitóides de ovos da família Scelionidae. As duas espécies são igualmente atacadas por *Polysphincta* sp. (Ichneumonidae), mas com uma baixa freqüência. *Baeus* sp. (Scelionidae) ataca preferencialmente as ootecas de *C. morretes*, o que pode constituir um dos fatores que explicam sua menor abundância no Parque Estadual de Intervales. Apresentamos ainda dois trabalhos descrevendo novas espécies de aranhas orbitelas coletadas durante a realização do capítulo 2, e um trabalho sinonimizando uma espécie de cleptoparasita que ocorre nas teias de *Cyclosa* e de várias outras espécies de aranhas orbitelas, em uma das áreas de estudo.

ABSTRACT

Spiders are attacked by a number of natural enemies. Predation and/or parasitism pressures may have influenced many behavioral characteristics, such as the permanence in shelters constructed in the periphery of orb-webs and the addition of web barriers. The stabilimenta added to the central portion of the orb-webs of many species of Araneidae, Tetragnathidae and Uloboridae, just like these other devices, may constitute a defensive component. The possible functions of these structures composed by silk and/or detritus, however, are subject of a intense discussion since their description, in the end of XIX century. Prey attraction, protection against the direct incidence of sun rays, stability, reduction of damage promoted by birds were some functions already proposed to explain the presence of stabilimenta. In this study we present a revision about predators and parasites of spiders and about the defenses used to minimize their success. In the second chapter we analyzed the prey collected by hunting wasps in two areas of Atlantic Forest in southeastern Brazil, comparing these data with prey availability in the field. The species composition of orb-web spiders and the size of prey captured by wasps indicated that prey selection is not based only on the relative abundance of spider species and on their size. Spiders that build stabilimenta, for example, were captured in a frequency much lower than the expected, suggesting that this structures may protect the spiders against hunting wasps. In the next chapter we presented data regarding the structural variability of the stabilimenta constructed by *Cyclosa fililineata* and by *Cyclosa morretes*. Detritus columns are more frequent for both species, but discontinuous linear structures (blobs of detritus) are relatively common in webs of males and juveniles of *C. morretes*. This last kind, as well as structures composed by silk (spiral and linear) constitute intermediate stages towards the construction of detritus columns. We observed a great variation in the position occupied by the spiders within the columns, what may reduce even more the efficiency of

attacks by visually oriented predators. Then we present a study testing the two main hypothesis about the functions of stabilimenta, the defense against predators and prey attraction. The results obtained suggest that the detritus structures of *C. morretes* and *C. fililineata* do not attract prey, but may reduce the frequency of attacks by possible predators. In the last chapter we investigated the occurrence of parasitism in juveniles and adults, by ichneumonids, and in egg sacs, by *Baeus* sp (Scelionidae). Both spider species are equally attacked by *Polysphincta* sp. (Ichneumonidae), but in a low frequency. *Baeus* sp. attacks preferentially egg sacs of *C. morretes*, what may constitute an important factor to explain the lower abundance of this species in P.E. Intervales. We also present two studies describing new species of orb-weavers collected during the surveys of chapter 2, and a study sinonimizing one species of kleptoparasite (*Argyrodes rigidus*, Theridiidae) usually found using webs of *Cyclosa* and other orb-weavers in P.E. Intervales.

Introdução



INTRODUÇÃO GERAL

Predadores e parasitas de aranhas possuem representantes em uma grande variedade de táxons, incluindo desde pequenos ácaros e nematóides até aves e mamíferos. Todos os estágios de maturação são vítimas de inimigos naturais. Os ovos são consumidos por dípteros, neurópteros, himenópteros predadores e por outras espécies de aranhas (Barnes *et al.* 1992, Gibson *et al.* 1997, Redborg 1998, Jackson & Pollard 1996, Jackson & Brassington 1987). As aranhas são susceptíveis ainda ao ataque de muitos parasitóides, especialmente himenópteros da família Scelionidae e da superfamília Chalcidoidea (Austin 1984, 1985; Fitton *et al.* 1987; Van Baarlen *et al.* 1994). Imaturos em estágios iniciais de desenvolvimento, além do canibalismo, estão sujeitos à predação por aranhas invasoras de teias (Coyle & Meigs 1992, Gonzaga & Vasconcellos-Neto 2002) e por vários predadores eventuais (e.g. saguis - Smith 2000). Finalmente, jovens e adultos são capturados por inúmeras espécies de invertebrados, como vespas-caçadoras e mantídeos, e de vertebrados (Schoener & Toft 1983, Schulz 2000, Stiles 1995). Além disso, são vítimas de dípteros endoparasitas (Schlinger 1987), himenópteros parasitóides (Fincke *et al.* 1987), nematóides (Poinar 1985), ácaros (Welbourn & Young 1988) e até mesmo alguns fungos que atacam exclusivamente aranhas (Evans & Samson 1987).

Em alguns casos, a predação pode reduzir significativamente a abundância e a diversidade de aranhas em um local. Spiller & Schoener (1988), por exemplo, demonstraram que a presença de lagartos dos gêneros *Ameiva* e *Anolis* é capaz de reduzir o número de espécies de aranhas em ilhas. Os lagartos podem levar pequenas populações locais à extinção ou limitá-las a níveis baixos o suficiente para que sejam extintas estocasticamente. Além disso, os lagartos competem com as aranhas por recursos alimentares, reduzindo a biomassa de presas disponível e, conseqüentemente, a fecundidade dessas últimas (Spiller & Schoener 1990). Ilhas sem lagartos apresentaram densidades de aranhas construtoras de teias até dez vezes maiores que ilhas que abrigavam populações de lagartos (Schoener & Spiller 1987).

A intensidade da pressão de predação sobre diferentes populações de uma espécie, entretanto, é muito variável. Um exemplo dessa variabilidade foi fornecido por Riechert & Hedrick (1990), estudando duas populações de *Agelenopsis aperta* (Agenelidae) que ocupam formações vegetais distintas. Como a abundância e a diversidade de aves são maiores na área com vegetação mais densa, a população de *A. aperta* deste local sofreu taxas de predação de 7 a 10 vezes maiores que a população de áreas abertas. Foram realizados, então, experimentos visando investigar possíveis diferenças entre o comportamento anti-predatório nas duas áreas. Os resultados mostraram que as aranhas da população submetida a constantes ataques demoravam mais para sair de seus refúgios após a percepção de estímulos que simulavam a aproximação de um predador. Descendentes de aranhas coletadas nessa população, criados em laboratório, também demonstraram uma resposta mais acentuada aos estímulos.

Assim como diferentes populações de uma mesma espécie, diferentes espécies em uma mesma área podem estar sujeitas a pressões de predação distintas. Vários fatores determinam a exposição de animais aos seus possíveis predadores, como a utilização e o tempo de permanência em abrigos (Sih 1992), a coloração do corpo (Vasconcellos-Neto & Gonzaga 2000) e a formação de grupos (Lima & Dill 1990, Seibt & Wickler 1990). Uma grande variedade de características morfológicas (como a presença de espinhos abdominais, pêlos urticantes e coloração críptica) e comportamentais (construção de abrigos, barreiras de fios, vibração das teias, entre outros) de diferentes espécies de aranhas, podem influenciar a freqüência com que são localizadas e capturadas.

Um grande número de adaptações contra predação em aranhas envolve o uso das teias (veja Cloudsley-Thompson 1995). A maioria das espécies, por exemplo, envolve seus ovos com camadas compactas de seda, o que dificulta o acesso de larvas de algumas espécies predadoras (Hieber 1992). Muitas constroem abrigos de seda em suas teias de captura. Neste caso, as aranhas podem permanecer em seu interior grande parte do tempo, como fazem algumas espécies da família Araneidae, ou refugiar-se apenas quando detectam a aproximação de um possível predador. Barreiras de fios de seda também são relativamente comuns. Formando uma estrutura tridimensional em torno da posição ocupada pela aranha, esses complexos de fios podem constituir um obstáculo à aproximação de vespas e um mecanismo de alerta, possibilitando a fuga da aranha antes de uma investida direta (Edmunds & Edmunds 1986, Blackledge *et al.* 2003).

Blackledge *et al.* (2003) atribuem a grande diversidade de aranhas construtoras de teias tridimensionais em Orbiculariae (clado que inclui as famílias Uloboridae, Deinopidae e o clado Araneiodea – veja Coddington 1990) à proteção que essas estruturas conferem contra vespas caçadoras. Em uma ampla revisão da literatura sobre os tipos de presas capturados por seis gêneros de vespas da família Sphecidae, esses autores observaram que aranhas construtoras de teias orbiculares constituem cerca de 76% dos itens presentes nos ninhos, embora sejam muito menos abundantes na natureza.

A forma bidimensional das teias orbiculares une a capacidade de amortecer a energia cinética do vôo de possíveis presas com a de retê-las por tempo suficiente para que a aranha possa aproximar-se e realizar a captura. Além disso, essas teias são relativamente pouco dispendiosas e podem ser consumidas diariamente, evitando o desgaste de suas propriedades adesivas. Isso permite que suas construtoras possam decidir se o sítio inicialmente escolhido para o forrageamento é satisfatório ou se, após um período de escassez de presas, torna-se necessário procurar um novo microhabitat (Shear 1986). Apesar dessas vantagens, o padrão bidimensional deixa suas construtoras totalmente expostas, o que explica a alta proporção de aranhas orbitelas nos ninhos de vespas.

Nem todas as aranhas construtoras de teias orbiculares, entretanto, permanecem no centro de suas teias. Muitas deslocaram sua posição para a periferia, repousando sobre a vegetação adjacente ou em abrigos compostos por folhas enroladas, teia e/ou detritos (Grasshoff & Edmunds 1979, Edmunds & Edmunds 1986). Esse deslocamento pode ser importante como uma defesa primária, reduzindo a probabilidade de localização das aranhas pelos predadores, e secundária (no caso da presença de refúgios), constituindo uma barreira mecânica à aproximação de inimigos naturais. Entre aquelas que ficam expostas no centro de suas teias orbiculares durante o dia, estão várias espécies construtoras de estabilimentos (Scharff & Coddington 1997).

Os estabilimentos adicionados às teias de vários gêneros das famílias Araneidae, Tetragnathidae e Uloboridae podem constituir outra modificação de uma estrutura orbicular simples para uma função defensiva. Essas estruturas, que são adensamentos de seda contendo ou não detritos (restos de presas, exúvias, matéria vegetal), foram inicialmente descritas como componentes adicionais de sustentação. Posteriormente várias outras possíveis funções foram sugeridas, como sinalizar a presença da teia para evitar sua destruição por aves (Horton 1980) e reduzir a exposição das aranhas ao sol (Humphreys 1992). A maioria dos trabalhos sobre essas estruturas, entretanto, sugere que seriam sinais utilizados para atrair presas ou para reduzir a predação, neste último caso, dificultando a localização da aranha (Eberhard 1973), constituindo barreiras contra vespas (Blackledge & Wenzel 2001) ou alterando o tamanho aparente das aranhas (Schoener & Spiller 1992).

A hipótese de atração de presas está baseada no estudo de Craig & Bernard (1990), que demonstra que as faixas de seda adicionadas ao centro das teias de aranhas do gênero *Argiope* refletem luz ultravioleta. Esses autores sugerem que esse padrão de reflexão pode atrair insetos polinizadores que estão buscando padrões similares refletidos por flores. Outra possibilidade seria que insetos confundissem os sinais visuais fornecidos pelos estabilimentos com espaços abertos, direcionando seu vôo para as teias. Vários trabalhos recentes apresentaram resultados congruentes com esta hipótese (e.g. Bruce *et al.* 2001, Herberstein 2000, Tso 1996 – mas veja Blackledge 1998, Blackledge & Wenzel 1999 para evidências contrárias). Por outro lado, a hipótese defensiva também é sustentada por muitos estudos. Blackledge & Wenzel (2001), por exemplo, demonstraram que duas espécies de vespas, *Chalybion caeruleum* e *Sceliphron caementarium* (Sphecidae), apresentam maior freqüência de fracassos durante tentativas de capturar *Argiope argentata* quando essas aranhas adicionaram estabilimentos às suas teias.

A polêmica em torno da função (ou funções) dos estabilimentos está, em grande parte, restrita às estruturas compostas unicamente por seda (Fig. 1). Embora tenham surgido independentemente várias vezes em Orbiculariae (Scharff & Coddington 1997), a maioria dos experimentos já realizados foi feita com estabilimentos de aranhas do gênero *Argiope*. Poucos estudos incluem estabilimentos com detritos e alguns autores sugerem que esses devem ser considerados como um fenômeno comportamental distinto (e.g. Herberstein *et al.* 2000). Observações de espécies dos gêneros *Allocyclosa* e *Cyclosa*, entretanto, sugerem que algumas aranhas descritas como construtoras de estabilimentos de detritos podem construir estruturas de seda quando não dispõe de restos de presas, exúvias e material vegetal (W.G. Eberhard no prelo, M.O. Gonzaga obs. pessoal).

Essas aranhas ficam permanentemente no centro de suas teias, em posição adjacente ao estabilimento. Apresentam um padrão de coloração e adotam posturas que as tornam praticamente imperceptíveis em meio aos detritos (Fig. 2). Embora essas características tenham sido atribuídas por vários autores à defesas contra predação (Eberhard 1990, Herberstein *et al.* 2000, Edmunds & Edmunds 1986), não existem estudos demonstrando sua eficiência em reduzir a freqüência de ataques ou o sucesso de captura por predadores.

No primeiro capítulo deste trabalho, é apresentado um panorama geral sobre predadores e parasitas de aranhas, assim como de várias estratégias de defesa utilizadas para dificultar seu sucesso na localização e captura de suas presas. O capítulo seguinte é dedicado às vespas caçadoras. Foram realizadas coletas em duas áreas florestais para determinar a abundância relativa de presas (espécies de aranhas construtoras de teias orbiculares) e compará-la com os itens encontrados nos ninhos de vespas. Em seguida, é apresentado um capítulo descritivo, sobre a variabilidade na forma, tamanho e composição dos estabilimentos construídos por duas espécies de *Cyclosa* em várias localidades. Esse capítulo inclui ainda resultados referentes ao processo de reconstrução de estabilimentos após a remoção das estruturas originais. No capítulo 4 os estabilimentos das duas espécies são testados em relação à sua capacidade de atrair presas e de reduzir a probabilidade de ataque por inimigos naturais. No quinto capítulo são apresentados dados relacionando a abundância relativa de *Cyclosa fililineata* e *C. morretes* a parâmetros de fecundidade e à freqüência de ataques por parasitóides. Os anexos 1 e 2 referem-se à descrição de novas espécies coletadas durante a realização dos trabalhos relativos ao capítulo 2. Finalmente, o anexo 3 apresenta uma sinonímia de um cleptoparasita que ocorre em teias de *Cyclosa* e de outros gêneros das famílias Araneidae e Tetragnathidae que ocorrem no Parque Estadual Intervales.

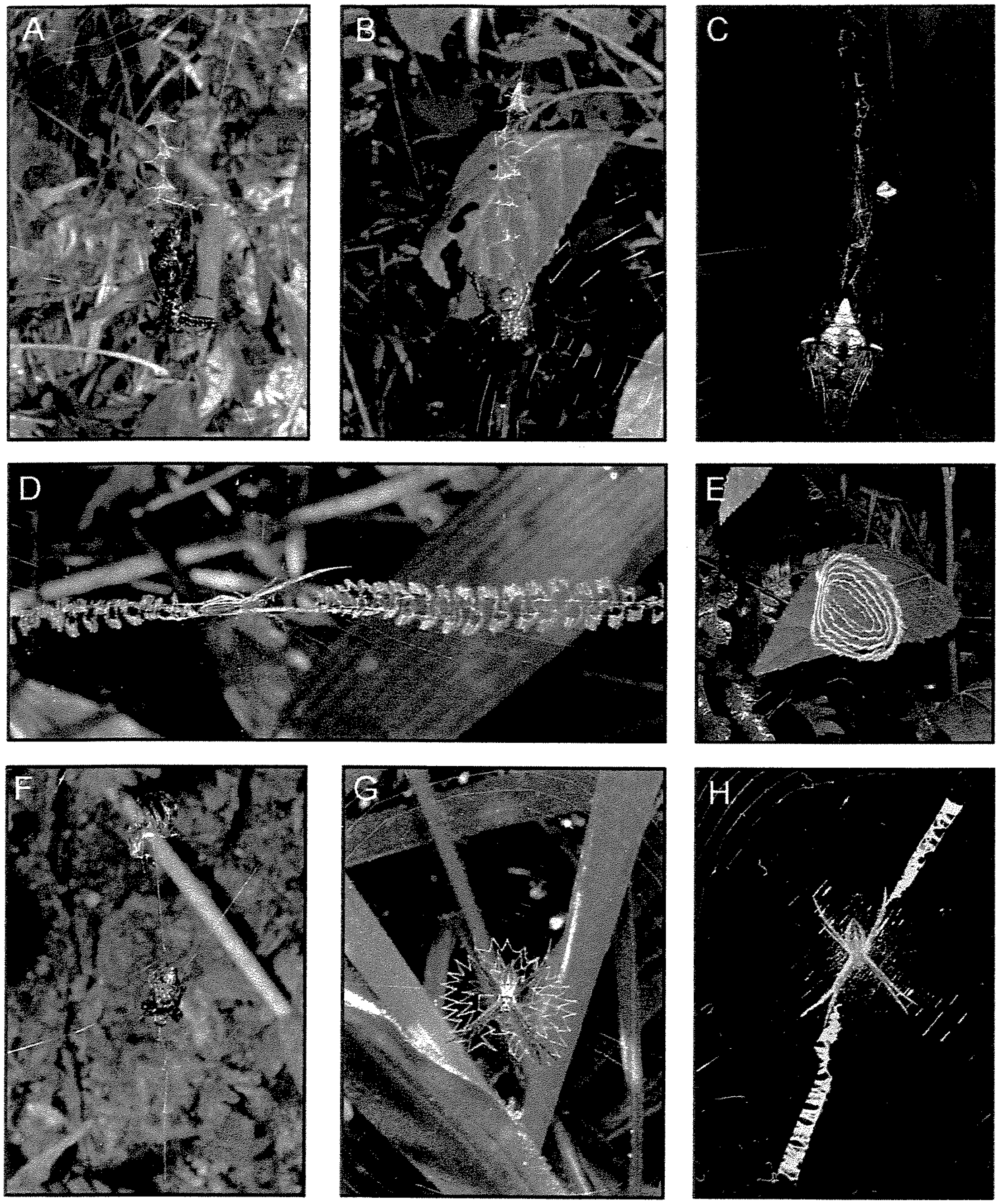


Fig.1: Estabilimentos de seda. (A) *Micrathena spitzi*, (B) *Micrathena plana*, (C) *Verrucosa arenata*, (D) e (E) Uloboridae não identificado, (F) *Cyclosa morretes*, (G) e (H) *Argiope argentata*.

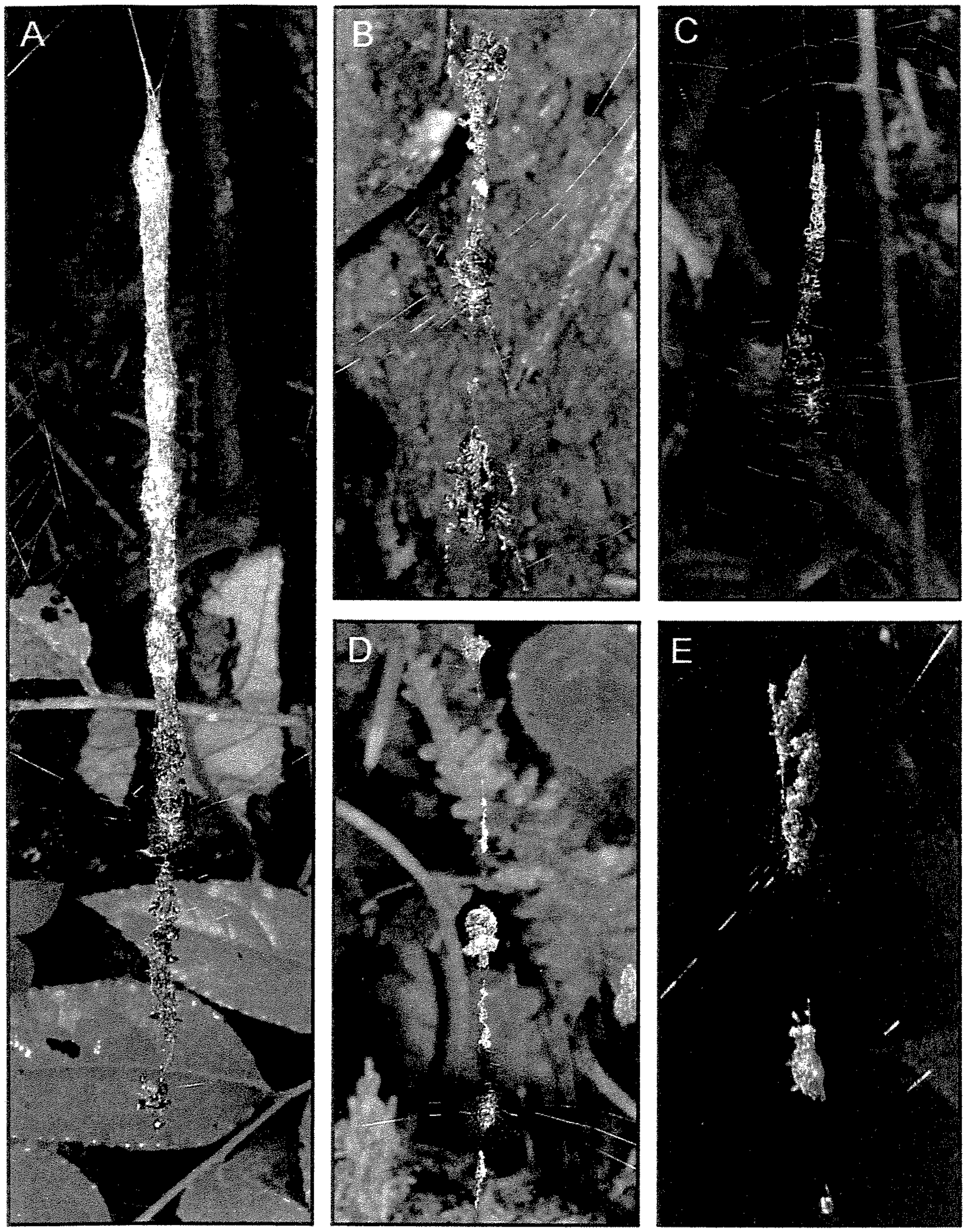


Fig.2: Estabilimentos com detritos construídos por *Cyclosa morretes*. (A) Estrutura linear com ootecas na porção superior, (B) estrutura com forma complexa, (C) estabilimento de seda sendo substituído por coluna de detritos, (D) e (E) estruturas descontínuas.

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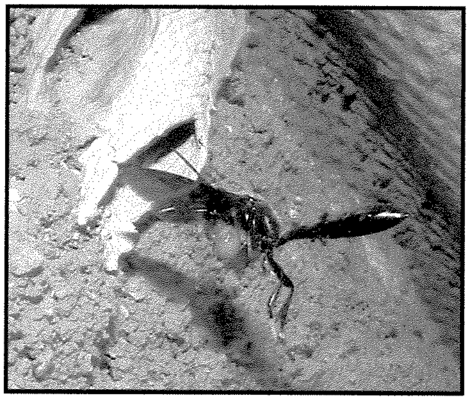
Capítulo 1

Inimigos naturais e defesas contra predação e parasitismo em aranhas



INIMIGOS NATURAIS E DEFESAS CONTRA PREDAÇÃO E PARASITISMO EM ARANHAS

Aranhas constituem um item importante na dieta de muitos predadores, sendo atacadas também por parasitas e parasitóides com diferentes graus de especificidade alimentar. A grande diversidade de hábitos de vida e variação de tamanho corporal no grupo permitiram sua utilização por um conjunto muito heterogêneo de inimigos naturais, incluindo vertebrados, muitos insetos, nematóides, ácaros e mesmo outras aranhas. Neste capítulo serão apresentados os principais predadores e parasitas de aranhas, assim como as principais estratégias de defesa utilizadas para evitar seu sucesso.

PARASITAS, PARASITÓIDES E PREDADORES

Nematóides

Existem casos documentados de parasitismo em aranhas por duas ordens de nematóides, Mermithida (família Mermithidae) e Rhabditida (famílias Steinernematidae e Heterorhabditidae). Esta última, entretanto, nunca foi encontrada em aranhas em condições naturais, ocorrendo normalmente como parasita de insetos (Poinar 1985).

Embora em laboratório indivíduos de dois gêneros de Rhabditida, *Neoaplectana* e *Heterorhabditida*, tenham mostrado-se capazes de infectar aranhas e se desenvolverem até a fase adulta, não foram capazes de se reproduzirem utilizando estes hospedeiros (Poinar & Thomas 1985). Isto pode indicar que aranhas realmente não são hospedeiros adequados a Rhabditida, mas é possível também que a ausência de registros seja conseqüência de uma característica muito particular de seu ciclo de vida. Representantes dos gêneros *Neoplectana* e *Heterorhabditida* apresentam bactérias simbiontes do gênero

Xenorhabdus nos intestinos das formas infectantes (de terceiro estadio). Estas bactérias contaminam o hospedeiro logo após a entrada do parasita, matando-o em cerca de 2 a 3 dias. O parasita completa seu desenvolvimento e se reproduz no corpo do hospedeiro morto. Esse curto intervalo entre a infecção e a morte torna a amostragem de aranhas parasitadas por estes nematóides muito mais improvável que a de indivíduos contendo parasitas que permanecem por um longo período com o hospedeiro vivo (Poinar 1987a), como é o caso dos Mermithidae.

Existem muitos registros, inclusive alguns fósseis, de espécies de Mermithidae parasitando aranhas (Poinar 1987a, Poinar & Early 1990, Poinar 2000), opiliões (Poinar *et al.* 2000) e pseudo-escorpiões (Poinar & Curcic 1992, 1994). Os Mermithidae apresentam basicamente dois tipos de ciclo de vida. No primeiro, indireto, as fêmeas depositam seus ovos na água e os ovos são ingeridos por insetos (larvas de Ephemeroptera ou Trichoptera), eclodindo em seus intestinos. Quando o inseto adulto é capturado por uma aranha o nematóide juvenil, até então em estado de dormência, torna-se ativo e continua seu desenvolvimento no corpo do novo hospedeiro (Poinar & Early 1990). Neste caso torna-se necessário ao parasita que o hospedeiro final retorne ao ambiente aquático para a oviposição, e existem indícios de que aranhas parasitadas por pelo menos uma espécie, *Aranimermis aptispicula*, realmente tendem a migrar para locais com água (Poinar 1987a). No segundo tipo de ciclo de vida, direto, os juvenis infectam o hospedeiro definitivo, crescem em seu corpo e emergem ainda como formas juvenis, completando o ciclo (maturação, acasalamento e oviposição) no ambiente externo (Poinar 1987a).

Dípteros endoparasitas

Dípteros da família Acroceridae depositam seus ovos em uma variedade de substratos (solo, galhos mortos, troncos de árvore, capim). As larvas eclodem de 3 a 6 semanas depois, iniciando sua busca por uma aranha hospedeira. Quando a aranha é localizada, a larva escala o corpo da hospedeira e, geralmente, posiciona-se na região anterodorsal do abdome, onde dificilmente pode ser alcançada. Nesse local produz um pequeno corte e entra no corpo da hospedeira, aparentemente permanecendo em um estado de diapausa até que a aranha atinja o penúltimo estágio de desenvolvimento. Parasitas de Araneomorphae podem ficar neste estado por um período de 6 a 9 meses, enquanto espécies parasitas de Mygalomorphae podem permanecer inativas no corpo das aranhas por até 10 anos (Schlinger 1987).

As larvas maduras (de quarto estádio) representam o estágio ativo, que ocasiona a morte do hospedeiro através do consumo de seus tecidos internos. Esse processo pode levar de 24 horas a mais de uma semana, mas normalmente a morte do hospedeiro ocorre apenas nas últimas 12 horas antes da emergência do parasitóide. A aranha constrói um abrigo de teia, semelhante àquele utilizado para a ecdise, pouco antes do início do período de atividade da larva. Esse abrigo é utilizado pela larva para fixar-se e empupar. Cerca de 1 a 3 semanas depois emerge o adulto (Schlinger 1987, Cady *et al.* 1993).

A freqüência de ataques por acrocerídeos é maior em aranhas de hábitos cursoriais e fossoriais, mais propensas a encontrarem as larvas infectantes. Entre as aranhas construtoras de teias, aquelas que permanecem mais próximas ao solo, visitam a vegetação constantemente e/ou apresentam muitos fios conectados ao substrato (e.g. Dipluridae, Agelenidae, Amaurobiidae, alguns Araneidae e Segestridae) são mais susceptíveis (Cady *et al.* 1993).

Dípteros predadores de ovos

Muitas famílias de Diptera (Drosophilidae, Chloropidae, Phoridae, Ephydridae, Rhinophoridae e Sarcophagidae) apresentam espécies predadoras de ovos de aranhas (veja Barnes *et al.* 1992, Disney & Evans 1979, Eason *et al.* 1967). Informações sobre a história de vida desses predadores, entretanto, são escassas e estão restritas a poucos grupos, como o gênero *Pseudogaurax* (Chloropidae).

A maioria das espécies de *Pseudogaurax,* cujas larvas alimentam-se de ovos de aranhas, apresenta baixa especificidade em relação às suas presas. As aranhas atacadas com maior freqüência pertencem às famílias Araneidae e Tetragnathidae (veja Barnes *et al.* 1992, Lockley & Young 1993). Algumas espécies, entretanto, já foram encontradas também em ootecas de Theridiidae e mesmo em casulos de Lepidoptera e ootecas de mantídeos (Barnes *et al.* 1992). *Pseudogaurax signatus*, uma das espécies mais comuns, foi descrita infestando ovos de *Latrodectus mactans* (Theridiidae) na Califórnia, EUA. Os ovos (15 a 45) são depositados na superfície da ooteca e cerca de cinco a seis dias depois as larvas rompem as camadas de seda que envolvem a massa de ovos. Durante os oito ou nove dias seguintes as larvas consomem os ovos e empupam, ainda dentro da ooteca. Os adultos emergem cerca de duas semanas depois e podem viver mais de 71 dias em condições de laboratório (Pierce 1942 *apud* Barnes *et al.* 1992).

Ácaros

A maioria dos ácaros encontrados em aranhas é forética, geralmente deutoninfas da subordem Astigmata. Entre as espécies parasitas estão muitos Prostigmata das famílias Erythraeidae, Trombidiidae e Eutrombidiidae, além de um gênero de

Mesostigmata, *Ljunghia*, descrito como ocorrendo obrigatoriamente associado a aranhas (Welbourn & Young 1988).

Neurópteros

Membros da subfamília Mantispinae (Neuroptera: Mantispidae) são essencialmente predadores de ovos de aranhas. As larvas de primeiro estádio de algumas espécies perfuram as ootecas e alimentam-se dos ovos através de um tubo formado pela mandíbula e maxila modificadas. Outras escalam as aranhas, permanecendo em seus corpos até a oviposição e início da construção da ooteca, quando então posicionam-se junto à massa de ovos e são envoltos por seda. Dentre essas últimas, a maioria utiliza o pedicelo das aranhas para fixação (embora algumas possam fixar-se nos pulmões) (Redborg 1998). Após a fixação, as larvas mantêm-se através da ingestão de hemolinfa, esperando até que os ovos estejam disponíveis (Redborg & Macleod 1983). Essas espécies geralmente são incapazes de perfurar as ootecas, mas algumas, como *Mantispa uhleri*, podem utilizar as duas estratégias (Redborg 1998).

As larvas localizam as aranhas colocando-se em postura forética, estendendo-se e oscilando o corpo em posição vertical. É possível que os encontros sejam fortuitos, mas existem poucas informações disponíveis sobre detalhes do mecanismo de busca das larvas (Redborg 1998). Sabe-se, entretanto, que seguram-se em diferentes hospedeiros, abandonando-os quando verificam que são inadequados (veja Batra 1972, Hoffman & Hamilton 1988).

Machos de aranhas também são hospedeiros inapropriados, uma vez que as larvas precisam entrar em contato com os ovos depositados pelas fêmeas. Quando encontram machos, entretanto, as larvas permanecem aderidas ao seu corpo esperando a oportunidade de transferência para uma fêmea durante a cópula ou durante um evento de canibalismo (O'Brien & Redborg 1997). Scheffer (1992), por exemplo, observou larvas de *Climaciella brunnea* entrando em atividade e movendo-se de machos para fêmeas de *Schizocosa ocreata* e *Schizocoza roverni* (Lycosidae), mas nunca no sentido oposto. Espécies que penetram diretamente nas ootecas, como *Mantispa viridis*, são atraídas por fios de teia, mas não demonstram nenhuma reação à aproximação das aranhas (Redborg 1998).

Depois de solucionados os problemas de localização e fixação no corpo das aranhas, as larvas têm ainda que lidar com outros fatores que podem comprometer seu sucesso. Permanecer por muito tempo sobre o corpo da aranha pode significar um grande risco de remoção e/ou predação. Redborg (1982) observou que *Mantispa uhleri* pode minimizar esses riscos acelerando o processo de desenvolvimento de seu hospedeiro (*Lycosa rabida*, Lycosidae). Em seu experimento, as fêmeas parasitadas atingiram a fase adulta com nove ou dez mudas, enquanto o grupo sem parasitas tornou-se maduro com dez ou onze. Uma vez dentro das ootecas surge mais um problema. A eclosão dos filhotes pode representar uma diminuição da disponibilidade de alimento e riscos de injúria para as larvas. No entanto, *Mantispa uhleri* aparentemente é capaz de evitar (provavelmente através de um controle químico) o desenvolvimento dos ovos, garantindo a provisão de alimento durante todo o período em que as larvas permanecem dentro da ooteca (Redborg 1983).

Fungos

Os fungos patógenos de aranhas restringem-se à ordem Clavicipitales de Ascomycotina e a alguns Hyphomycetes (Deuteromycotina). Dentre esses últimos, alguns, como os do gênero *Gibellula* e *Clathroconium*, são encontrados ocorrendo exclusivamente em aranhas (Evans & Samson 1987).

A maioria das infecções inicia-se no abdome, parte menos espessa do exoesqueleto das aranhas, envolvendo mecanismos de penetração física e enzimática. Uma vez dentro do hospedeiro, inicia-se a produção de toxinas letais (Evans & Samson 1987).

Nentwig (1985), trabalhando no Panamá, observou que aranhas da família Araneidae atacadas por fungos freqüentemente são encontradas em plataformas de seda similares àquelas presentes nas teias durante as mudas. É possível que a construção dessa estrutura seja desencadeada pela infecção, já que os espécimes observados eram adultos e as teias não continham sinais de exúvias. Se isto de fato ocorre, deve haver um intervalo de pelo menos dois dias entre a infecção e a morte das aranhas (Nentwig 1985a).

Himenópteros

Várias famílias de Hymenoptera (Diapriidae, Encyrtidae, Eulophidae, Eupelmidae, Eurytomidae, Ichneumonidae, Pompilidae, Pteromalidae, Scelionidae, Signiphoridae e Sphecidae) incluem espécies que utilizam ovos ou as próprias aranhas para alimentação de suas larvas. As estratégias utilizadas são muito variadas. As larvas podem se desenvolver dentro da ooteca, destruindo toda a massa de ovos, ou dentro de cada ovo individualmente. Aranhas jovens e adultas podem ser capturadas para provisionar os ninhos antes da oviposição, permanecendo apenas imobilizadas para constituir alimento fresco para as larvas. Mas, geralmente, cada espécie de vespa limita-se a poucos grupos de presas ou hospedeiros, por restrições relacionadas ao habitat utilizado, ao tamanho das aranhas e/ou a outras características morfológicas das presas disponíveis (como presença de espinhos abdominais) (Austin 1985, Cloudsley-Thompson 1995, Fitton *et al.* 1987).

Scelionidae

Enquanto muitos membros da família Scelionidae utilizam lepidópteros ou heterópteros como hospedeiros, alguns gêneros da subfamília Scelininae (*Ceratobaeus, Idris, Baeus,* entre outros) consomem exclusivamente ovos de aranhas (Austin 1984, 1985). Austin (1984) descreve o comportamento de oviposição de duas espécies de *Ceratobaeus*, *C. masneri* e *C. clubionus*, que utilizam ovos de aranhas da família Clubionidae. Esses parasitóides entram nos abrigos construídos pelas aranhas e introduzem seus longos ovipositores dentro dos ovos, atravessando as camadas de seda da ooteca. Quando localizam alguma abertura, utilizam-na para obter acesso direto aos ovos. Apesar disso, nem todos são alcançados e cerca de 30 a 40% deles (localizados no centro da ooteca) sempre permanecem intocados. Os parasitóides continuam consumindo os ovos mesmo durante a fase de pupa, emergindo como indivíduos adultos e copulando logo em seguida.

Parasitóides dos gêneros *Baeus, Idris e Hickmanella* também depositam seus ovos dentro dos ovos de aranhas. Ao contrário de *Ceratobaeus*, espécies do gênero *Baeus* possuem ovipositores curtos e são morfologicamente adaptados para escavar e penetrar nas ootecas. Utilizam principalmente ovos de aranhas das famílias Araneidae, Linyphiidae e Theridiidae (Van Baarlen *et al.* 1994). Representantes do gênero *Idris* penetram em ootecas de várias famílias, entre elas Theridiidae, Lycosidae, Salticidae e Uloboridae (Austin 1985, Fitton *et al.* 1987). Eason *et al.* (1967) acompanharam todo o processo de oviposição e desenvolvimento das larvas de uma espécie de *Idris*, parasitóide de *Pardosa lapidicina* (Lycosidae). Essas aranhas produzem cerca de 35 ovos por ooteca e, destes, uma média de 28 foram utilizados por *Idris*. Aparentemente apenas ovos com menos de 72 horas de idade são atacados. O desenvolvimento leva de 21 a 22 dias e os parasitóides parecem só sair da ooteca quando a aranha produz uma abertura para liberar seus filhotes. Depois disso, podem viver de 10 a 13 dias em condições de laboratório.

Superfamília Chalcidoidea (Encyrtidae, Eulophidae, Eupelmidae, Eurytomidae, Signiphoridae e Pteromalidae)

Esse grupo apresenta uma grande diversidade de hábitos alimentares. Algumas famílias de Chalcidoidea são exclusivamente fitófagas (e.g. Agaonidae, cujas espécies estão associadas com figos, e Tanaostigmatidae, que são galhadores). Outras, como Eurytomidae, apresentam gêneros com espécies fitófagas e gêneros cujas espécies incluem tecidos animais em sua dieta. Os Chalcidoidea atacam 13 ordens de insetos, ácaros, nematóides e ootecas de aranhas e de pseudoescorpiões (Gibson *et al.* 1997).

Existem duas estratégias de ataque a ootecas de aranhas. Espécies da família Encyrtidae (e.g. *Proleurocerus, Amira*) são essencialmente parasitóides, completando seu desenvolvimento dentro dos ovos das aranhas. Neste caso, cada larva consome apenas um ovo. (Austin 1985, LaSalle 1990). Já em Pteromalidae, Eupelmidae e Eurytomidae todas as espécies provavelmente são predadoras. As larvas movimentam-se livremente dentro das ootecas, consumindo vários ovos. Na família Eulophidae existem predadores de ovos e parasitóides destes predadores. Seis gêneros da subfamília Tetrastichinae (*Aprostocetus*, *Arachnoobius*, *Aranobroter*, *Baryscapus*, *Tachinobia* e *Tetrastichus*) foram coletados em ootecas de aranhas. Os hospedeiros incluem espécies das famílias Araneidae (*Mastophora*, *Metepeira* e *Parawixia*), Clubionidae (*Clubiona*), Salticidae (*Phidipus*), Theridiidae (*Latrodectus*) e Thomisidae (*Misumena* e *Philodromus*) (LaSalle 1990).

Ichneumonidae

"... Parece-me existir sofrimento demais no mundo. Não posso persuadir-me de que um Deus beneficente e onipotente tenha propositadamente criado os ichneumonídeos com a expressa intenção de alimentarem-se no interior dos corpos ainda vivos de lagartas...". Nesta sentença, extraída de uma carta escrita à Asa Gray, em 1860, Charles Darwin expressa o quanto os hábitos alimentares das larvas dessas vespas o incomodavam. Entretanto, as larvas de lepidópteros, cujo sofrimento tanto angustiava Darwin, não são as únicas vítimas dos Ichneumonidae. Suas larvas alimentam-se também de ovos (gêneros *Clistopyga*, *Tromatobia*, *Zaglyptus*, *Gelis*, *Aclastus*, entre outros) e de aranhas jovens e adultas (tribo Polysphinctini da subfamília Pimplinae) (Fig. 1.1). Em relação a estas últimas existe, inclusive, um registro fóssil de cerca de 20-40 milhões de anos (Poinar 1987b).

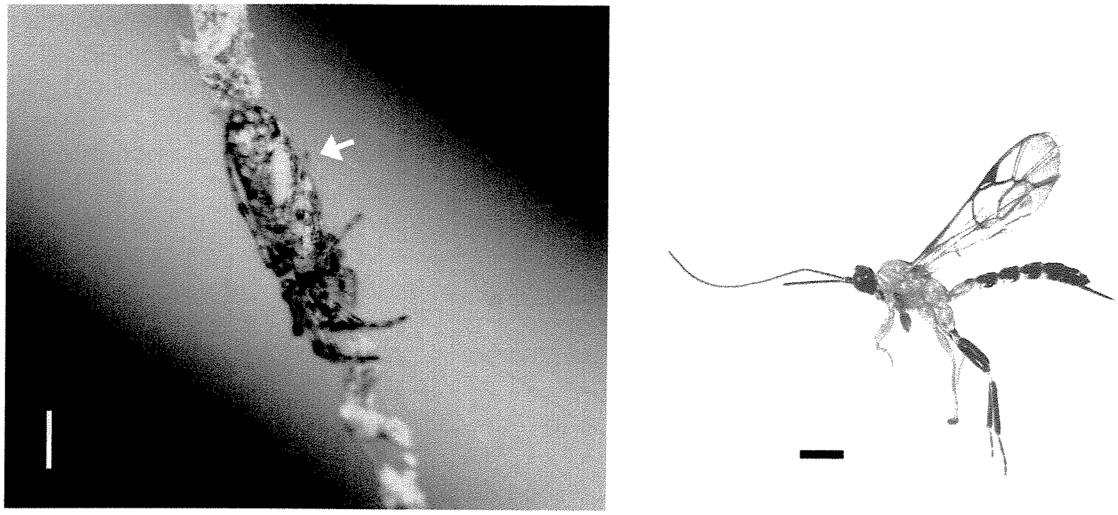


Fig.1.1: Larva de *Polysphincta* sp. (Ichneumonidae) presa ao dorso do abdome de *Cyclosa fililineata* e vespa adulta. Escalas: 1mm. Fotos: M.O.Gonzaga.

Fincke *et al.* (1990) descrevem o processo de oviposição de uma vespa da tribo Polysphinctini, *Hymenoepimecis* sp., em *Nephila clavipes*. Inicialmente a aranha é paralisada com uma picada entre o esterno e a coxa. Em seguida a vespa segura-se no dorso de seu abdome, move o ovipositor durante cerca de 5 minutos (possivelmente para verificar se a aranha já está parasitada e obter informações sobre seu tamanho) e deposita um único ovo na superfície do tegumento da aranha. Depois de 15 minutos a aranha já está totalmente recuperada da ação do veneno. Durante a primeira semana a larva cresce vagarosamente, mas após duas semanas o hospedeiro já foi completamente consumido. O sucesso das larvas em completar seu desenvolvimento depende do tamanho da aranha e, em alguns casos, a biomassa disponível não é suficiente. Apesar disto, fêmeas com tamanhos intermediários apresentaram a maior freqüência de parasitismo, o que pode indicar que os indivíduos maiores conseguem impedir a oviposição sobre seus corpos. Machos raramente são parasitados, provavelmente por não representarem uma oferta de alimento suficiente para que as larvas se desenvolvam.

Eberhard (2000a, 2000b, 2001) descreve um caso particularmente interessante de manipulação do hospedeiro (*Plesiometa argyra*, Araneidae) por outra espécie do mesmo gênero, *Hymenoepimecis argyraphaga*. Após a oviposição, as aranhas continuam suas atividades normais durante um período de 7 a 14 dias, enquanto ocorre a eclosão do ovo e o crescimento da larva. Esta permanece alimentando-se de hemolinfa até pouco antes de sua terceira muda. Na noite que precede a morte da aranha, a larva (de segundo estádio) induz a aranha a construir de uma teia modificada, especialmente adequada à fixação do casulo que será construído para empupar. Essas mudanças comportamentais do hospedeiro são promovidas quimicamente e a remoção das larvas permite que as aranhas retornem gradualmente à construção de teias normais.

Vespas caçadoras

Várias espécies da família Sphecidae e todas de Pompilidae capturam aranhas para provisionar seus ninhos. Em Sphecidae cada larva é alimentada com várias pequenas aranhas. Essa estratégia permite o transporte das presas até o ninho, previamente construído. Além disso, a disponibilidade de presas pequenas geralmente é maior e os riscos envolvidos no processo de captura e transporte são menores. Os Pompilidae capturam aranhas grandes, freqüentemente com tamanho corporal superior ao seu próprio. Isso praticamente inviabiliza o transporte da presa por longas distâncias e muitas espécies iniciam a construção do ninho somente após a captura (Coville 1987, Martins 1991a). Outras nem chegam a transportar as aranhas. Procuram-nas em seus refúgios e, após imobilizá-las com seu veneno, depositam um ovo. As larvas consomem as aranhas e empupam ainda dentro do refúgio construído por suas hospedeiras (O´Neil 2001). Algumas espécies de Pompilidae são parasitas sociais e podem ainda explorar os esforços de provisionamento desempenhados por outras espécies da mesma família. Este é o caso, por exemplo, de *Evagetes mohave*. Esta espécie procura os ninhos construídos por *Anoplius apiculatus autunnalis*, cava até alcançar a presa previamente armazenada (um indivíduo de *Arctosa littoralis*, Lycosidae), destrói e/ou alimenta-se do ovo previamente depositado por *Anoplius* e, finalmente, deposita seu próprio ovo sobre o abdome da aranha (Evans *et al.* 1953). Dois outros gêneros, *Ceropales* e *Irenangelus*, apresentam comportamentos semelhantes. *Ceropales*, entretanto, persegue outros Pompilidae enquanto estes ainda estão transportando suas presas. Quando surge uma oportunidade, insere seu ovipositor nos pulmões foliáceos da aranha e deposita um ovo. Esse ovo eclode rapidamente e a larva destrói o ovo depositado pela vespa que estava transportando a presa (Evans *et al.* 1953, O´Neill 2001).

Sphecidae

As subfamílias Sphecinae (gêneros *Sceliphron* e *Chalybion*) e Larrinae (*Miscophus*, *Pisonopsis*, *Pison* e *Trypoxylon*) apresentam espécies que capturam aranhas para o provisionamento de seus ninhos. São, em geral, solitárias e todas as espécies apresentam atividade diurna. Os ninhos podem ser cavados no solo, construídos com barro (Fig.1.2) ou modificados a partir de cavidades pré-existentes. São compostos por várias células individualizadas, cada uma contendo um ovo e aranhas em número suficiente para promover o desenvolvimento da larva até que esteja pronta para empupar. Esse número depende da abundância relativa de aranhas com diferentes tamanhos e pode variar de apenas 2 (M.O. Gonzaga, obs. pess.) a mais de 40 (Coville & Coville 1980). O ovo fica aderido ao abdome de uma das aranhas e a eclosão ocorre de 1,5 a 3,5 dias após a oviposição. O consumo de toda a biomassa contida na célula ocorre em poucos dias e as aranhas permanecem vivas durante todo esse período, embora imobilizadas pelo veneno injetado pela vespa durante a captura (Coville 1987).

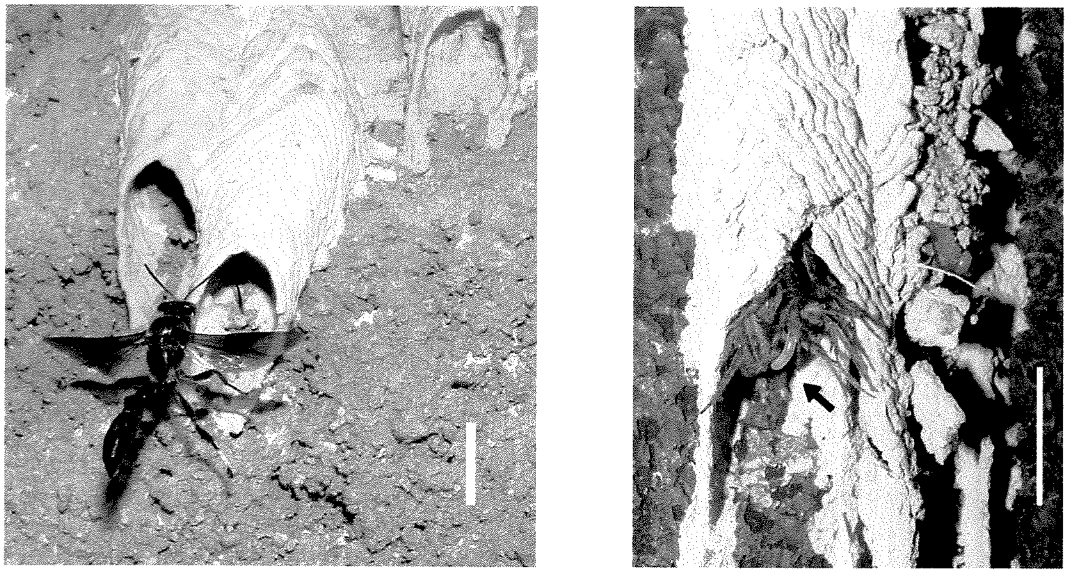


Fig.1.2: *Trypoxylon albonigrum* construindo ninho de barro e detalhe com secção de ninho já provisionado com aranhas. A seta indica a larva da vespa. Escalas: 1cm. Fotos: M.O.Gonzaga.

A seleção de presas por Sphecidae parece basear-se principalmente em dois critérios: a abundância relativa e o tamanho das aranhas (Coville 1987). No entanto, algumas espécies capturam preferencialmente, ou mesmo exclusivamente, determinadas famílias. É o caso, por exemplo, de *Trypoxylon xanthandrum*, que captura apenas aranhas da família Senoculidae (Coville & Griswold 1983) e de *T. politum*, cujas presas restringem-se quase que somente a três gêneros da família Araneidae (*Neoscona*, *Araneus* e *Eustala*) (Rehnberg 1987). Outras, como *Trypoxylon* (*Trypargilum*) *lactitarse* e *Trypoxylon* (*Trypargilum*) *rogenhoferi*, utilizam presas de muitas famílias, construtoras de diferentes tipos de teias e mesmo de hábitos cursoriais (Camilo & Brescovit 1999a, b). Blackledge *et al.* (2003) realizaram uma compilação de todas as presas capturadas por Sphecidae registradas em estudos publicados desde o início do século passado. A grande maioria das presas (principalmente dos gêneros *Trypoxylon* e *Sceliphron*, que representam o maior número de trabalhos) é de aranhas construtoras de teias orbiculares, bidimensionais.

As estratégias de captura variam muito. *Sceliphron caementarium*, por exemplo, persegue as aranhas que saltam de suas teias após perceberem sua aproximação. Já *Chalybion caeruleum* pousa sobre a teia ou no substrato em que ela está fixada e usa suas pernas para puxar os fios, provocando uma vibração que atrai as aranhas em sua direção. Ao aproximarem-se as aranhas são capturadas ou perseguidas enquanto retornam ao centro da teia (Blackledge & Pickett 2000).

Pompilidae

Enquanto várias espécies de Sphecidae utilizam vários outros tipos de presas (veja Martins 1991b, Field 1992), os Pompilidae capturam exclusivamente aranhas para provisionar seus ninhos (Evans 1953, Martins 1991b). A única exceção descrita na literatura é a espécie *Salius sycophanta*, que foi observada provisionando seus ninhos com solífugas do gênero *Galeodes* (Galeodidae) (Cloudsley-Thompson 1958, 1977). Outra diferença importante entre as duas famílias é que, em Pompilidae, cada larva alimenta-se apenas de uma aranha. Após a imobilização da presa, com inoculação de veneno e algumas vezes com a remoção das pernas, a vespa a transporta até um ninho previamente construído ou a um local adequado para o início da construção. Em seguida deposita um ovo, geralmente sobre o abdome da aranha, e fecha o ninho. Os locais de nidificação são os mais variados, incluindo cavidades pré-existentes, superfícies de solo descoberto, solo sob a serrapilheira ou até mesmo o interior de formigueiros, cupinzeiros e tocas de tatus abandonadas (Martins 1991a, b).

Alguns gêneros de Pompilidae são muito seletivos em relação às suas presas. *Pedinaspis*, *Aporus* e *Psorthaspis*, por exemplo, provisionam seus ninhos apenas com aranhas da família Ctenizidae (Evans 1953). Já *Tachypompilus* captura Lycosidae (Evans 1953), Pisauridae e Sparassidae (Martins 1991a). *Episyron*, *Batazonellus*, *Calicurgus* e *Poecilopompilus* geralmente utilizam Araneidae (Evans 1953), embora algumas espécies possam desviar-se desse padrão (Martins 1991a). A especialização em relação ao tipo de presa fornecido às larvas pode levar ao desenvolvimento de estratégias de caça muito particulares. *Poecilopompilus mixtus*, por exemplo, utiliza uma tática baseada no comportamento de fuga de suas presas, que saltam das teias quanto são atacadas. Rayor (1996) descreve freqüentes ataques a colônias de *Metepeira incrassata* (Araneidae), nos quais essas vespas voam entre os fios do complexo de teias. A vibração provocada por seu deslocamento faz com que várias aranhas saltem, presas apenas por um fio guia. As aranhas são atacadas enquanto ainda suspensas no ar e perseguidas assim que chegam ao solo. Quando a aranha não é prontamente localizada a vespa inicia uma busca pelo solo, aparentemente sendo capaz de perceber sinais olfativos de sua presa. O sucesso de captura dessa estratégia é relativamente baixo se comparado ao de outras vespas, que atacam diretamente as aranhas enquanto estas ainda estão nas teias. No entanto, o investimento na captura é proporcional ao tamanho das presas e aranhas grandes geralmente não conseguem escapar.

Polis *et al.* (1998) analisaram o impacto de Pompilidae na densidade de aranhas orbitelas em várias ilhas no Golfo da Califórnia e observaram que as vespas podem ser responsáveis por uma expressiva redução da densidade das aranhas. Esta redução, entretanto, ocorreu apenas em anos com pluviosidade suficiente para proporcionar boas floradas e, conseqüentemente, abundância de alimento para as vespas adultas. Além da disponibilidade de alimento para os adultos, outros fatores podem influenciar o tamanho populacional e a riqueza de vespas caçadoras, como a existência de microhabitats adequados para nidificação (Quinn *et al.* 1995) e a incidência de parasitismo e predação sobre os ninhos (Tscharntke *et al.* 1998).

Aranhas

Muitas espécies podem eventualmente capturar outras aranhas, mas o desenvolvimento de estratégias de caça específicas e a utilização preferencial do grupo é mais rara. O hábito araneofágico é amplamente difundido na família Mimetidae (Fig.1.3), e existem também casos bem documentados entre Salticidae (com destaque para o gênero *Portia*), Pholcidae, Theridiidae e Archaeidae.

Algumas espécies apresentam estratégias de forrageamento específicas para a invasão de teias e captura de suas construtoras. Como suas presas muitas vezes são também predadoras em potencial, essas aranhas desenvolveram complexos comportamentos para que não sejam detectadas durante a invasão ou para que não sejam percebidas como uma ameaça. Podem, por exemplo, imitar o padrão de vibração de presas interceptadas pela teia da aranha que intencionam atacar. Este é o caso de

Mimetus maculosus (Mimetidae), uma espécie da Nova Zelândia que ataca aranhas de várias famílias. Após localizar a teia de uma possível presa, *M. maculosus* faz uma pausa nos fios marginais e, em seguida, começa a produzir vibrações de diferentes tipos e intensidades com suas pernas. Durante o tempo em que permanece parada a invasora pode obter informações sobre as características da teia, a localização da aranha residente e seu tamanho. A qualidade dessas informações, entretanto, varia muito de acordo com o tipo de teia, o que implica em diferentes probabilidades de sucesso de captura. *M. maculosus* geralmente é mais eficiente quando invade teias de aranhas ecribeladas, conseguindo evitar a aderência na substância viscosa presente nestas teias. As vibrações produzidas após o período exploratório constituem sinais que visam estimular o movimento da residente em direção à invasora. A residente reage como se a fonte de vibrações fosse um pequeno inseto e aproxima-se para a captura, quando então é atacada e envolta em fios (Jackson 1992a, Jackson & Whitehouse 1986). Esse tipo de comportamento é considerado um mimetismo agressivo, no qual a espécie araneofágica manipula o comportamento da presa através de estímulos vibratórios característicos de outros organismos.

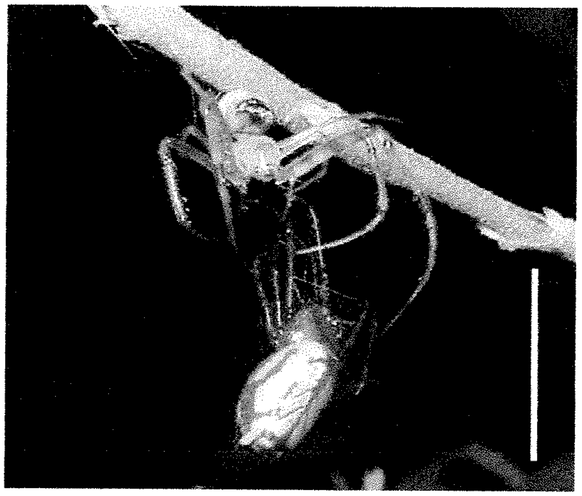


Fig.1.3: *Gelanor* sp. (Mimetidae) capturando uma fêmea de *Leucauge* sp. (Tetragnathidae). Escala: 1cm. Foto: M.O.Gonzaga.

Mas é entre os Salticidae que encontram-se as espécies araneofágicas com comportamentos predatórios mais complexos e melhor estudados. Dez espécies da subfamília Spartaeinae (gêneros *Brettus*, *Gelotia*, *Cyrba* e *Portia*) utilizam mimetismo agressivo para capturar outras aranhas (Jackson 1990a, b, Jackson 1992a, Jackson & Hallas 1986a, b). Outro gênero da mesma subfamília, *Cocalus*, foi observado invadindo teias e consumindo suas ocupantes, embora sem produzir sinais vibratórios. Essas espécies podem andar sobre teias de aranhas cribeladas e ecribeladas e possuem uma característica que é especialmente útil para localizar e identificar suas presas em potencial: enxergam muito bem (veja Forster 1982a, b). Enquanto a maioria das espécies de aranhas araneofágicas depende exclusivamente dos sinais vibratórios promovidos pelas residentes para obter informações sobre seu tamanho, identidade e localização, os Salticidae, com seus grandes olhos e complexas retinas, podem fazê-lo de forma muito mais eficiente. Além disso, a complexidade dos sinais emitidos pelos mímicos é muito maior, incluindo variedades específicas para muitos tipos diferentes de presas.

Outros predadores invertebrados

Vários outros predadores invertebrados, sobretudo insetos, já foram observados alimentando-se de aranhas. Mantídeos (Mantodea: Mantidae), por exemplo, atacam *Argiope keyserlingi* (Araneidae) posicionando-se em folhas próximas às teias e saltando em sua direção ou, quando estão próximos o suficiente, apenas estendendo suas pernas dianteiras raptoriais (Herberstein & Heiling 2001). Bruce *et al.* (2001) também observaram mantídeos capturando *A. keyserlingi* e demonstraram que esses predadores usam o sinal visual fornecido pelas decorações das teias (estabilimentos) para localizar as aranhas. Gonzaga (dados não publicados) registrou esses predadores consumindo outra espécie de Araneidae, *Alpaida quadrilorata*, e invadindo colônias de *Anelosimus jabaquara* (Theridiidae).

Formigas também constituem predadores importantes de algumas espécies de aranhas. Vieira & Höfer (1994) analisaram os restos de presas encontrados em colônias de duas formigas de correição na Amazônia, *Eciton burchelli* e *Labidus praedator*. Aranhas representaram 13% das presas da primeira e 17% da segunda espécie. *Eciton* raramente capturou aranhas construtoras de teias e cursoriais muito pequenas (Anapidae, Ochyroceratidae, Oonopidae), mas exerceu forte pressão de predação sobre aranhas cursoriais com tamanho corporal entre 1 e 2 cm, principalmente do gênero *Ctenus*. Já *L. praedator* utilizou um espectro mais amplo de presas, incluindo Araneidae, Caponidae, Dipluridae, entre outras, embora *Ctenus* spp. também tenha constituído o grupo de aranhas mais abundante entre suas presas. Formigas que patrulham árvores também encontram aranhas com freqüência e invadem suas teias (Edmunds & Edmunds 1986, Henschel 1998). Cerca de 60% das colônias de *Stegodyphus dumicola* (Eresidae), por exemplo, são atacados por formigas (*Anoplolepis steigroeveri*) durante os meses de verão em uma área na periferia do deserto do Kalahari. As formigas matam todas as aranhas nos ninhos, destroem as ootecas e capturam os indivíduos que conseguem fugir para o solo (Henschel 1998).

Polis *et al.* (1998) apontam o escorpião *Centruroides exilicauda* (Buthidae) como um dos principais predadores de aranhas orbitelas nas ilhas do golfo da Califórnia, e Polis & Hurd (1995) observaram que a densidade de aranhas em ilhas onde esta espécie está presente é significativamente menor. Aranhas também foram itens freqüentes na dieta de *Paruroctonus mesaensis*, espécie que ocorre em dunas, na Califórnia, EUA (McCormick & Polis 1986).

Predadores vertebrados

Mesmo aves que consomem preferencialmente outros recursos alimentares, como néctar ou frutos, freqüentemente incluem artrópodes em sua dieta (veja Poulin & Lefebvre 1996). Segundo Stiles (1995), esse hábito pode ser especialmente importante para suprir as necessidades protéicas das fêmeas durante o período em que estão produzindo ovos. Stiles analisou a importância relativa de diferentes grupos de artrópodes na alimentação de várias espécies de beija-flores na Estação Biológica de La Selva, na Costa Rica. Vários grupos foram utilizados, mas aranhas representaram de 70 a 95% das presas capturadas por membros da subfamília Phaethorninae. Os dados para quatro espécies desta subfamília mostraram que três delas, *Phaethornis superciliosus*, *Glaucis aenea* e *Eutoxeres aquila*, capturam preferencialmente aranhas construtoras de teias, enquanto *Threnetes aenea* captura uma grande proporção de Salticidae. Poulin *et al.* (1994) também registrou a utilização de aranhas por várias outras espécies de beija-flores na Venezuela.

Gunnarsson (1996, 1998) realizou experimentos comparando áreas expostas com áreas livres da presença de aves, demonstrando que esses predadores podem reduzir significativamente a densidade de aranhas em um sistema florestal temperado. Riechert & Hedrick (1990) também observaram uma alta incidência de predação de aranhas (*Agelenopsis aperta*, Agelenidae) por aves em uma floresta no Arizona, EUA. Além do impacto causado pela predação, as aves podem também diminuir a abundância de presas para as aranhas e influenciar sua distribuição de tamanhos, capturando preferencialmente indivíduos maiores (Gunnarson 1998).

Lagartos também estão entre os principais predadores vertebrados. Schoener & Toft (1983) observaram que a densidade de aranhas em ilhas das Bahamas onde não existem lagartos é muito maior que a densidade em ilhas onde ocorrem esses predadores. Para determinar se essas diferenças na densidade poderiam realmente ser provocadas por predação, Spiller & Schoener (1988) conduziram um experimento excluindo lagartos de algumas áreas cercadas e mantendo outras inalteradas. Quatro meses após o início do experimento o número de espécies e a abundância de aranhas nas áreas controle já era significativamente menor e o mesmo padrão repetiu-se nos meses seguintes. Spiller & Schoener (1990) demonstraram ainda que existe uma grande sobreposição na dieta de lagartos e aranhas nessas ilhas, e que a competição por recursos pode ser responsável por uma redução na taxa de crescimento e fecundidade das aranhas. Outros experimentos de exclusão confirmam o grande impacto da presença de lagartos sobre a abundância de aranhas orbitelas (Dial & Roughgarden 1995, Pacala & Roughgarden 1984). Além disso, listas de itens consumidos por várias espécies de lagartos apresentam aranhas entre os itens mais freqüentes (e.g. Pianka 1970, Vitt 1991, Vitt & Carvalho 1992, Vitt *et al.* 2001). Wise & Chen (1999) ressaltam, entretanto, que a maior parte das evidências da regulação da densidade de aranhas por vertebrados refere-se a espécies construtoras de teias. Esses autores demonstraram que a densidade de aranhas do gênero *Schizocosa* (Lycosidae) no solo de uma floresta secundária nos EUA não aumenta como conseqüência da exclusão de predadores vertebrados.

Aranhas são consumidas ainda por diversas espécies de mamíferos. Smith (2000), por exemplo, registrou a captura de aranhas por duas espécies de saguis, *Saguinus mystax* e *S. fuscicollis* no Peru. Além de capturar indivíduos adultos, a primeira foi vista alimentando-se também de ovos e filhotes. Constituem a segunda categoria na preferência do musaranho *Sorex cinereus* (McCay & Storm 1997) e a primeira de *S. minutus* (Churchfield & Brown 1987). Estão também entre as presas mais capturadas por alguns morcegos (Shiel *et al.* 1991, Schulz & Wainer 1997). Entre estes, a espécie que apresenta dieta mais especializada é *Kerivoula papuensis* (Vespertilionidae). Aranhas (principalmente das famílias Araneidae e Tetragnathidae, construtoras de teias orbiculares) foram encontradas em 99,1% das amostras de fezes dessa espécie, estando presentes também entre os dentes de 63% dos indivíduos coletados por Schulz (2000).

Finalmente, são predadas também por anfíbios (e.g. Bellocq *et al.* 2000, Hirai & Matsui 2001, Jesus *et al.* 1998) e peixes (Figiel & Miller 1994, Suter & Gruenwald 2000). Entre as 58 espécies de anuros analisadas por Parmelee (1999) na Amazônia peruana, os pequenos hilídeos foram o grupo com a maior proporção de aranhas em sua dieta. Os peixes capturam aranhas que utilizam a superfície da água para caçar. Pisaurídeos do gênero *Dolomedes*, por exemplo, ocorrem em diversos tipos de habitats aquáticos (lagos, riachos com fluxo lento, rios com corredeiras). Caçam hemípteros, salamandras e pequenos peixes (Krupa & Sih 1998), utilizando as ondas provocadas pelo movimento desses animais como estímulos táteis (Bleckmann & Lotz 1987). A utilização desse habitat para caça, entretanto, permite sua captura por alguns peixes maiores (Suter & Gruenwald 2000).

DEFESA

As estratégias de defesa dependem dos hábitos de vida (cursorial, construtor de teia) das aranhas, da intensidade de predação e de características comportamentais dos predadores e parasitóides. O tipo de estímulo (visual, químico, tátil) utilizado pelo predador para a detecção de suas presas, por exemplo, pode determinar o sucesso ou não de uma determinada tática empregada pelas aranhas. As defesas variam desde permanecer imóvel e adotar uma postura que esconde o contorno do corpo até a ameaça de agressão. Muitas espécies constroem refúgios, outras atiram-se de suas teias quando ameaçadas. A seguir serão descritos os principais tipos de mecanismos de defesas já identificados. Revisões mais extensas sobre este assunto podem ser encontradas em Cloudsley-Thompson (1995) e Edmunds & Edmunds (1986).

Refúgios e barreiras de teia

Várias espécies permanecem grande parte de sua vida em refúgios (Fig.1.4), como bromélias, buracos no solo e reentrâncias sob cascas de árvores, reduzindo sua exposição a predadores ao tempo necessário ao forrageamento e à procura por parceiros sexuais. Em alguns casos o próprio refúgio pode funcionar como uma armadilha para presas, como acontece com as Mygalomorphae conhecidas como aranhas-de-alçapão (e.g. *Ummidia*, *Bothriocyrtum*, *Cyclocosmia*). Essas aranhas cavam buracos no solo e fecham as entradas com portas móveis de seda, extremamente inconspícuas e freqüentemente camufladas com galhos, musgos e/ou folhas. Insetos que aproximam-se da abertura do refúgio são rapidamente capturados e transportados para o seu interior, onde ocorre o consumo. Apesar de praticamente não saírem de seus abrigos, essas aranhas são atacadas por vespas da família Pompilidae, que as localizam tateando o solo com suas antenas. Como uma defesa adicional contra os invasores, *Stanwellia nebulosa* (Nemesiidae) coloca uma pelota de terra em uma câmara na parede de sua toca. Esta pelota pode ser movida, fechando a aranha na porção inferior do buraco e impedindo o acesso de predadores. Já *Aname* sp. (Nemesiidae) constrói uma saída alternativa que permite uma rota de fuga caso a toca seja invadida (Preston-Mafhan & Preston-Mafhan 1993).

Fig.1.4: .Abrigo de teia construído por *Aglaoctenus lagotis* (Lycosidae). Escala: 1cm. Foto: M.O.Gonzaga.

A utilização de abrigos de seda, folhas e/ou detritos, também é muito comum em aranhas construtoras de teias. Muitas aranhas orbitelas, que não podem contar com a proteção de uma estrutura tridimensional de fios de teia, freqüentemente permanecem durante o dia em abrigos de seda e/ou folhas na periferia da espiral de captura (Figs.1.5 e 1.6). Os imaturos de *Metazygia laticeps* (Araneidae), por exemplo, constroem um abrigo de teia em gavinhas. Quando a aranha atinge um tamanho corporal incompatível com o seu abrigo, passam a adicionar uma folha seca presa aos fios de sustentação, onde escondem-se. As teias possuem um setor livre de espirais e um raio que vai do abrigo até o centro, permitindo que a aranha receba os sinais vibratórios das presas interceptadas sem que precise ficar exposta (M.O. Gonzaga, obs. pess.).

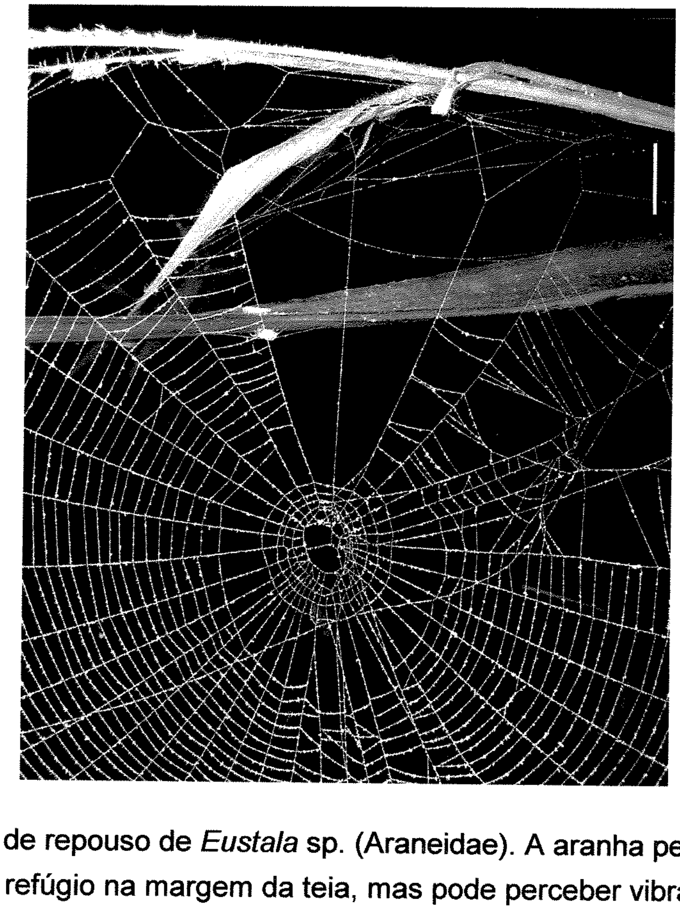


Fig. 1.5: Posição de repouso de *Eustala* sp. (Araneidae). A aranha permanece protegida em um refúgio na margem da teia, mas pode perceber vibrações através de um fio conectado ao centro. A seta indica a perna da aranha segurando este fio. Escala: 1cm. Foto: M.O. Gonzaga.

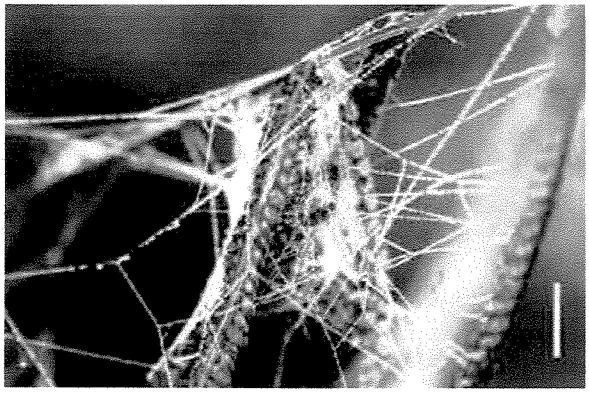


Fig. 1.6: Abrigo com folhas enroladas construído por *Araneus venatrix* (Araneidae). Escala 1cm. Foto: M.O. Gonzaga.

Barreiras de fios presentes em teias de algumas espécies das famílias Araneidae e Tetragnathidae e teias tridimensionais também podem representar obstáculos e tornar a aproximação de predadores perceptível a uma maior distância, permitindo a fuga das aranhas. Edmunds & Edmunds (1986) consideram que as barreiras de fios de *Nephilengys cruentata* e *Nephila* spp.(Tetragnathidae), *Cyrtophora citricola* (Araneidae), entre outras, têm como principal função defender as aranhas de predadores e não de sustentar as teias. Blackledge *et al.* (2003) sugerem que a pressão de predação por vespas da família Sphecidae pode ter constituído um importante fator direcionando a transformação do modelo orbicular bidimensional para teias tridimensionais em muitas espécies. Esta afirmação é sustentada principalmente pelos registros das presas preferencialmente capturadas por estas vespas (aranhas construtoras de teias orbiculares são 476% mais comuns como presas, embora 400% menos abundantes considerando-se a disponibilidade em vários ambientes) e pela coincidência dos registros fósseis. As primeiras teias tridimensionais modificadas a partir de estruturas orbiculares típicas surgiram no período Cretáceo, aproximadamente na mesma época do surgimento dos primeiros Sphecidae. Além disso, o número de presas capturadas por cada vespa para o provisionamento de seus ninhos é muito alto, o que sugere que os Sphecidae podem representar um fator de impacto significativo nas populações de suas presas (veja Blackledge *et al.* 2003 e referências citadas neste).

Além de adicionarem barreiras às teias de captura, muitas aranhas mantêm também suas ootecas protegidas por essas estruturas ou ao menos suspensas por fios, evitando assim o contato com o solo ou vegetação. Hieber (1992) demonstrou que manter a ooteca suspensa, em *Mecynogea lemniscata* (Araneidae) e *Argiope aurantia*, reduz o ataque por predadores generalistas (como formigas). Os ovos destas espécies contam ainda com a proteção de um denso invólucro de seda e de uma camada espessa de fios. A remoção experimental do invólucro externo proporcionou uma maior freqüência de predação por larvas de *Mantispa viridis* (Neuroptera: Mantispidae), indicando que constitui uma eficiente barreira mecânica à penetração das larvas dessa espécie. Esta barreira, entretanto, não é capaz de deter o Ichneumonidae *Tromatobia ovivora rufopectus*, que a perfura com seu longo ovipositor. Neste caso é a camada interna de fios entrelaçados que diminui o sucesso do predador, dificultando o acesso direto à massa de ovos (Hieber 1992).

Camuflagem

Muitos predadores utilizam a visão para localizar suas presas e a similaridade entre os padrões de coloração do corpo das aranhas e o substrato onde habitualmente se encontram pode reduzir a freqüência com que são encontradas. Existem vários exemplos de padrões crípticos de coloração, postura e formas do corpo em aranhas. Em Hersilidae, a pigmentação e a forma achatada do corpo tornam as aranhas muito semelhantes às cascas de árvores onde permanecem a maior parte do tempo (Cloudsley-Thompson 1995, Preston-Mafhan & Preston-Mafhan 1998). Muitos Salticidae também apresentam formas e cores que dificultam sua localização. *Portia schultzi*, por exemplo, apresenta pêlos, espinhos e uma forma de corpo tão modificada que, quando em repouso, assemelha-se a uma folha seca (Preston-Mafhan & Preston-Mafhan 1998). Já *Cyclosa* spp. (Araneidae) têm a mesma coloração que os detritos que adicionam às suas teias, permanecendo com as pernas retraídas em meio a eles durante o dia (Eberhard 1990, Neet 1990).

Espinhos e outras modificações morfológicas

Espinhos e abdomes rígidos podem constituir defesas mecânicas contra aves e vespas (Cloudsley-Thompson 1995). Freeman & Johnston (1978), por exemplo, observaram que vespas da espécie *Sceliphron assimile* (Sphecidae) parecem ignorar aranhas do gênero *Gasteracantha*, que possuem abdome com espinhos, enquanto capturam vários outros gêneros de aranhas construtoras de teias orbiculares. No entanto, *Gasteracantha* faz parte da lista de presas de outras espécies de vespas (veja Jiménez & Tejas 1994, Edmunds 1990), assim como *Micrathena*, outro gênero que apresenta muitos espinhos abdominais (veja Levi 1985, Gonzales-Bustamante 1994). A eficácia dos espinhos como estruturas defensivas ainda precisa ser testada, mas existe ainda uma outra característica morfológica dessas aranhas que pode reduzir sua susceptibilidade a possíveis predadores. O tegumento do abdome relativamente espesso provavelmente faz com que espécies de *Gastheracantha* sejam inadequadas como alimento para os primeiros estágios larvais de algumas vespas. Elgar & Jebb (1999) observaram que aranhas deste gênero são capturadas por *Sceliphron laetum* (Sphecidae) apenas após a captura de outras espécies com exoesqueleto menos espesso. Desta forma, as larvas podem iniciar sua alimentação com presas macias, passando para os itens alimentares de difícil digestão em estágios posteriores.

Talvez a modificação mais notável seja a da caranguejeira *Cycloscomia truncata* (Ctenizidae), uma aranha-de-alçapão que possui a região posterior do abdome achatada e muito rígida. A porção mais profunda de suas tocas estreita-se de forma a permitir que a aranha possa bloquear completamente a passagem com seu corpo, expondo apenas o escudo abdominal (Preston-Mafhan & Preston-Mafhan 1993). Este comportamento de bloquear a entrada do refúgio com uma parte do corpo já foi também descrito para várias espécies de formigas e é chamado de phragmosis (veja Brandão *et al.* 2001, Hölldobler & Wilson 1990).

Mimetismo

A semelhança morfológica de algumas espécies de aranhas com formigas (Cushing 1997, Oliveira 1986), mutilídeos (Nentwig 1985), pseudo-escorpiões (Platnick 1984), coleópteros (Chang 1996) e outros modelos não palatáveis ou agressivos pode evitar sua captura por predadores visualmente orientados que geralmente não incluem os modelos em sua dieta.

Estabilimentos

Estabilimentos são estruturas densas de seda e/ou detritos adicionadas às teias orbiculares de algumas espécies das famílias Araneidae, Tetragnathidae e Uloboridae (veja Herberstein *et al.* 2000, Scharff & Coddington 1997). Estas estruturas foram originalmente descritas como elementos de estabilização, sendo supostamente construídas para reforçar as conexões entre os fios da região central das teias (McCook 1889 apud Eberhard 1973).

Várias outras possíveis funções foram propostas desde então, como dificultar a localização por predadores visualmente orientados (Eberhard 1973, Neet 1990, Eberhard 1990), sinalizar a presença da teia para evitar sua destruição por aves durante o vôo (Horton 1980, Eisner & Nowicki 1983), fornecer sustentação para a aranha durante a ecdise (Nentwig & Rogg 1988), atrair presas (Craig 1991, Craig & Bernard 1990, Craig et al. 2001, Herberstein 2000, Tso 1996, 1998, Watanabe 1999) e propiciar um refúgio contra a exposição direta ao sol (Humphreys 1992). As grandes variações de forma e composição, entretanto, indicam que provavelmente estas estruturas não desempenham apenas uma única função (Neet 1990, Eberhard 1990, Cloudsley-Thompson 1995).

Blackledge & Wenzel (2001) investigaram a relação entre a presença de estabilimentos em teias de *Argiope trifasciata* e a susceptibilidade das aranhas à predação por duas vespas da família Sphecidae e verificaram que aranhas que adicionavam a estrutura de seda às teias tinham maior probabilidade de sobreviver aos ataques. Os autores sugerem que os estabilimentos podem constituir distrações que interferem na habilidade das vespas em atacar diretamente seu alvo. Schoener & Spiller (1992) observaram que estabilimentos em forma de cruz são construídos em maior freqüência por indivíduos médios de *Argiope argentata*, o que pode aumentar seu tamanho aparente para os lagartos predadores. Para as aranhas grandes a decoração das teias não traria benefícios e as pequenas poderiam aparentar o tamanho ótimo para predação. Por outro lado, é possível que os estabilimentos representem sinais visuais úteis à orientação de predadores, como aranhas do gênero *Portia*. Seah & Li (2001) demonstraram que *Portia labiata*, quando confrontada com teias com e sem estabilimentos, invadem preferencialmente as primeiras. Além disso, atacam com maior freqüência as teias que apresentam essas estruturas com formas previamente conhecidas, o que fornece um indício da importância da existência de diferentes formas.

Estabilimentos de *Cyclosa* spp. (Araneidae) apresentam uma característica bem distinta daqueles construídos por *Argiope* (Fig.1.7). Enquanto os estabilimentos de *Argiope* são compostos unicamente por seda, os de *Cyclosa* contém detritos e restos de presas em sua composição. Os detritos são dispostos de forma que o contorno da aranha torna-se praticamente imperceptível, e podem ser úteis para dificultar sua localização por predadores visualmente orientados.

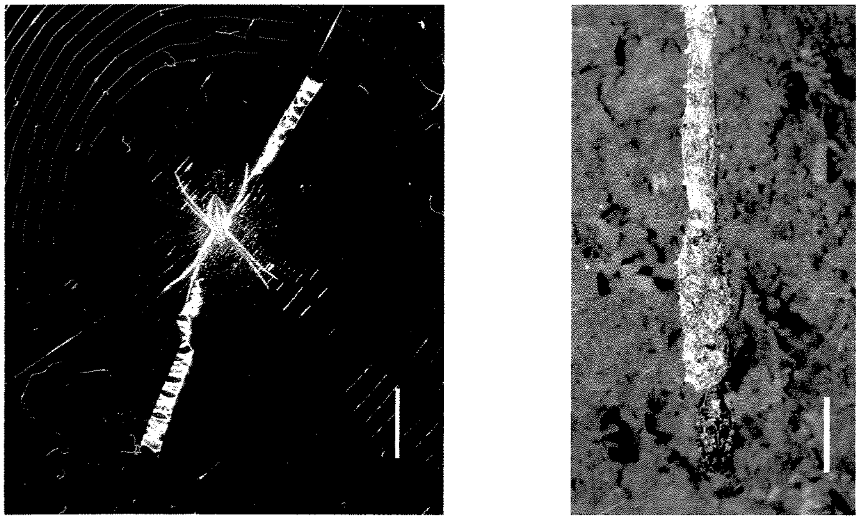


Fig.1.7: Estabilimentos de *Argiope argentata* e *Cyclosa morretes*. Escalas: 1cm. Fotos: M.O. Gonzaga.

Fuga, mudanças de coloração e tanatose

Atirar-se ao solo ou à vegetação em situações de risco é um comportamento muito comum em espécies construtoras de teias (e.g. Blackledge & Pickett 2000, Rayor 1996). Em alguns casos este comportamento está associado à mudança de coloração para um padrão mais escuro, semelhante ao substrato, e à tanatose (Edmunds & Edmunds 1986). O movimento pode ser um estímulo visual importante para os predadores e fingindo-se de mortas ou mesmo reduzindo a atividade as aranhas dificultam muito a sua localização. Persons *et al.* (2001) expuseram *Pardosa milvina* (Lycosidae) a substratos onde haviam estado indivíduos de *Hogna helluo* (Lycosidae) que alimentaram-se de *Pardosa* e à substratos onde estas aranhas alimentaram-se de grilos. As pistas químicas resultantes da predação sobre sua espécie foram suficientes para fazer com que *P. milvina* permanecesse um tempo significativamente maior sem demonstrar nenhum movimento.

Um exemplo interessante de comportamento antipredatório ligado à fuga foi fornecido por Riechert & Hedrick (1990), estudando duas populações de *Agelenopsis aperta* submetidas a diferentes pressões de predação por aves. Estas aranhas constroem teias em forma de funil, com uma área plana de interceptação de presas e um tubo que é utilizado como abrigo. As aranhas permanecem na saída do tubo, esperando que um inseto fique preso à malha de interceptação, mas correm para o interior do abrigo em reposta a alterações repentinas de luminosidade e sinais vibratórios. As aranhas da população exposta ao menor risco de predação voltam à posição de forrageamento após um distúrbio mais rapidamente que aquelas da área de alto risco. A resposta comportamental dos filhotes de fêmeas coletadas nas duas áreas, frente a estímulos vibratórios simulando a aproximação de aves, também foi diferente. Os filhotes provenientes da população com maior risco de predação apresentaram uma maior freqüência de fuga, indicando uma base genética determinante desse comportamento.

Teias coletivas

A formação de agregados pode minimizar o risco individual de predação reduzindo a probabilidade de localização (efeito de encontro) e de captura de cada membro do grupo após o encontro (efeito de diluição). Além disso, agregados e teias coloniais geralmente apresentam uma estrutura de fios (e algumas vezes folhas, galhos e detritos) mais complexa que as teias individuais (veja Tietjen 1986), o que pode constituir uma barreira física à aproximação do predador ou denunciar sua presença, possibilitando a fuga das aranhas (Uetz & Hieber 1994).

O efeito de encontro ocorre porque a detecção das presas não aumenta proporcionalmente com o tamanho do grupo. Uetz & Hieber (1994), por exemplo, não observaram ataques por vespas a aranhas solitárias e pequenos grupos de *Metepeira incrassata* (Araneidae), enquanto grupos maiores eram vítimas de ataques freqüentes. Embora a probabilidade de localização dos agregados fosse maior, grandes agregados eram atacados em uma taxa menor que a esperada considerando apenas o número de indivíduos. Essa inexistência de uma relação linear entre o tamanho do agregado e a probabilidade de encontro pode ser uma conseqüência da aparência visual de grupos de teias com diferentes tamanhos. A partir de um certo tamanho os grupos tornariam-se detectáveis pelos predadores, mas sua conspicuidade não aumentaria proporcionalmente ao número de novas aranhas.

Uma vez localizado o grupo, a probabilidade de cada indivíduo ser predado decresce conforme aumenta o tamanho da agregação. Neste caso, entretanto, o risco de predação depende da posição ocupada pelo indivíduo. Posições centrais podem significar uma menor exposição, sendo preferencialmente ocupadas. Alves-Costa & Gonzaga (2001) analisaram a distribuição espacial de *Philoponella vittata* (Uloboridae) em teias de vários hospedeiros e mostraram que o centro dos agregados é ocupado por aranhas grandes, enquanto indivíduos menores são deslocados para a periferia. Rayor & Uetz (1990, 1993) demonstraram que, em agregados de *M. incrassata*, aranhas situadas em posições periféricas são mais atacadas por vespas caçadoras. Embora as aranhas menores (e mais jovens) sejam obrigadas a ocupar locais mais expostos, beneficiam-se da maior disponibilidade de alimento nestes locais.

A vida em grupo pode também trazer alguns problemas em relação à proteção contra inimigos naturais. Henschel (1998) comparou a susceptibilidade à predação e ataque por fungos em aranhas solitárias e grupos de *Stegodyphus dumicola* (Eresidae) na Namíbia. Indivíduos solitários foram mais vulneráveis ao ataque por formigas e aves, porém a probabilidade da colônia ser destruída por fungos aumentou com seu tamanho e idade. Avilés & Tufiño (1998) registraram uma incidência relativamente alta de parasitismo, por uma vespa da família Eulophidae, em grandes colônias de *Anelosimus eximius* (Theridiidae). Da mesma forma, Hieber & Uetz (1990) observaram uma crescente incidência de parasitismo de ootecas de *M. incrassata,* pela mosca *Arachnidomya lindae* (Sarcophagidae), com o aumento do tamanho dos agregados. O mesmo padrão, entretanto, não foi encontrado para *M. atascadero.* Para esta espécie Hieber & Uetz (1990) encontraram uma grande flutuação na incidência de parasitismo de ano para ano, não havendo relação com o número de indivíduos no grupo. Para estes autores, grandes grupos em regiões tropicais estariam sempre mais sujeitos ao parasitismo, enquanto em ambientes temperados o padrão dependeria do comportamento das aranhas, tipos de parasitóides e estabilidade do habitat.

Cuidado maternal

Quase todas as aranhas envolvem seus ovos com fios de teia, formando um invólucro que ajuda a mantê-los unidos e que, na maioria dos casos, é capaz de manter condições adequadas de umidade e temperatura. Além disso, camadas compactas de seda podem constituir barreiras mecânicas contra parasitas (Foelix 1996). Muitas espécies, no entanto, vão além do fornecimento de um invólucro. As ootecas podem ser transportadas até a eclosão dos filhotes e mesmo ativamente protegidas contra predadores (incluindo machos canibais - veja Schneider & Lubin 1997) e parasitóides (veja Horel & Gundermann 1992, Li *et al.* 1999, Vannini *et al.* 1986). Em vários casos o cuidado é estendido para o período após a eclosão. Em aranhas da família Lycosidae, por exemplo, os filhotes sobem no corpo da mãe logo após deixarem a ooteca e são transportados enquanto permanecem segurando seus pêlos abdominais (Foelix 1996). As fêmeas de *Argyrodes flavipes* (Theridiidae) defendem seus filhotes contra a aproximação de coespecíficos atacando qualquer membro da colônia que se aproxime (Whitehouse & Jackson 1998). Reações agressivas similares foram observadas por Marques *et al.* (1998) para *Anelosimus jabaquara*.

Além da proteção através de comportamentos agressivos direcionados a possíveis predadores, muitas espécies fornecem também ninhos construídos com seda e, algumas vezes, folhas e detritos (veja Downes 1994, Evans 1998, Marques *et al.* 1998). Esses ninhos podem fornecer proteção mecânica contra a aproximação de predadores e parasitóides (Seibt & Wickler 1990), embora, em alguns casos, possam também abrigar inimigos naturais (Gonzaga & Vasconcellos-Neto 2001, Henschel 1998).

Pêlos urticantes

Alguns gêneros de Theraphosidae neotropicais apresentam pêlos urticantes em seus abdomes (*Avicularia*, *Pachistopelma*, *Acantoscurria*, *Lasiodora*, entre outros) (Fig.1.8) ou nos palpos (*Ephebopus*) (Bertani & Marques 1996, Marshall & Uetz 1990). Quando ameaçadas por predadores as aranhas da subfamília Theraphosinae esfregam o abdome com as pernas posteriores, liberando os pêlos no ar (Cooke *et al.* 1972, Pérez-Miles & Prandl 1991). O contato dos pêlos com a mucosa respiratória e os olhos dos predadores provoca grande irritação, evitando assim que as aranhas sejam capturadas. *Theraphosa leblondi* apresenta ainda o comportamento de incorporar os pêlos abdominais às suas ootecas, o que foi interpretado por Marshall (1992) como uma forma de camuflar a ooteca contra predadores especializados que utilizam sinais olfativos para distinguir entre a fêmea e os ovos. Já os Aviculariinae (com exceção de *Ephebopus*, que também lança os pêlos no ar) apenas direcionam o abdome para o agressor. Essas aranhas possuem pêlos de um tipo diferente, mais longo e robusto que os encontrados em Theraphosinae, capazes de penetrar a pele de possíveis predadores (Bertani & Marques 1996).

Fig.1.8: Theraphosidae com pêlos urticantes no abdome. Escala: 1cm. Foto: M.O. Gonzaga.

Produção de sons de advertência

A produção de sons já foi registrada em 26 das 109 famílias de aranhas e pode estar relacionada a cortejos, interações agressivas entre coespecíficos e defesa (Uetz & Stratton 1982). Entre os sons interpretados como defensivos estão os produzidos pelos órgãos estridulatórios de Theraphosidae, similares aos sons de advertência produzidos por algumas serpentes (Marshall *et al.* 1995, Uetz & Stratton 1982). Hinton & Wilson (1970) sugerem que os sons emitidos por *Micrathena gracilis* (Araneidae) também tem função defensiva, uma vez que podem ser registrados quando as aranhas são perturbadas. Apesar disto, pouco se sabe sobre o quanto a estridulação realmente é efetiva contra a predação.

Posturas agressivas e substâncias tóxicas

A adoção de posturas agressivas não é uma estratégia de defesa muito comum em aranhas. Apesar disto, algumas espécies como *Dysdera* spp. (Dysderidae), *Atrax* spp. (Hexathelidae) e *Phoneutria nigriventer* (Ctenidae) (Fig.1.9), freqüentemente reagem à presença de possíveis predadores com agressividade (Cloudsley-Thompson 1995). É interessante observar que a postura agressiva está associada à presença de venenos muito potentes. Além do veneno, algumas aranhas contam ainda com a eliminação de outros compostos tóxicos para afugentar seus inimigos. *Scytodes* spp. (Scytodidae), por exemplo, conhecidas como aranhas cuspideiras, podem lançar uma substância pegajosa que tem função de capturar presas e, possivelmente, também de proteção (Cloudsley-Thompson 1995).

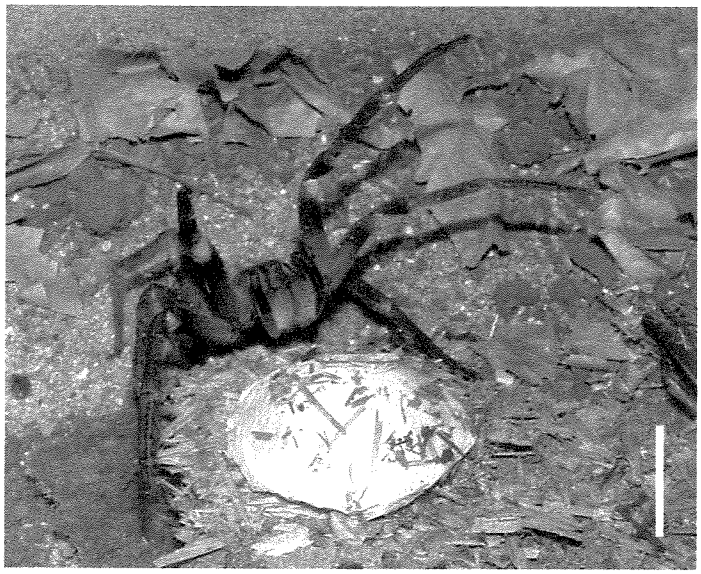


Fig.1.9: *Phoneutria nigriventer* protegendo sua ooteca com a demonstração de uma postura agressiva. Escala: 1cm. Foto: M.O.Gonzaga.

Vibração

Quando perturbadas, algumas aranhas das famílias Pholcidae (Jackson *et al.* 1990, Jackson *et al.* 1993) e Araneidae (Edmunds & Edmunds 1986, Jackson 1992b) vibram seus corpos vigorosamente, o que dificulta a determinação de sua posição exata por possíveis predadores. *Pholcus phalangioides* (Pholcidae), além desse comportamento que se estende por poucos minutos, desenvolveu ainda uma variação especificamente contra aranhas da família Salticidae que invadem suas teias. Heuts *et al.* (2001) realizaram uma série de experimentos apresentando várias espécies de aranhas a indivíduos de *P. phalangioides* e observaram que, na presença dos Salticidae, eles vibravam o corpo em uma freqüência moderada durante horas ou até mesmo dias.

Autotomia

Punzo (1997) realizou um experimento oferecendo aranhas (*Schizocosa avida*, Lycosidae) para o escorpião *Centruroides vittatus* e observou que a maioria dos indivíduos que escaparam (78%) conseguiu fazê-lo descartando uma perna. As aranhas fugiam enquanto o escorpião se alimentava da perna removida. Formanowicz (1990) também observou a autotomia de pernas em outra espécie, *Kukulcania hibernalis* (Filistatidae), quando confrontada com o mesmo escorpião. Para esta espécie, entretanto, perder pernas não garante uma maior probabilidade de sobrevivência em encontros com seu outro predador, o centípede *Scolopendra polymorpha* (Scolopendridae).

CONCLUSÕES

Embora tenhamos conhecimento da existência de um grande número de predadores, parasitas e parasitóides de aranhas, poucos foram intensivamente estudados. Interações comportamentais tão complexas quanto a manipulação de hospedeiros para construção de suportes de teia apenas começaram a ser investigadas e, certamente, muitas permanecem desconhecidas. Mesmo temas abordados com maior freqüência na literatura, como a possível proteção fornecida pela construção de estabilimentos e o provisionamento dos ninhos por vespas, ainda apresentam aspectos importantes a serem investigados. Em muitos casos, a descrição de comportamentos de defesa e estratégias utilizadas pelos predadores para captura estão baseadas em dados sobre poucas espécies, o que compromete quaisquer generalizações. Além disso, algumas regiões geográficas, como a Neotropical, foram muito pouco exploradas e praticamente nada se sabe sobre alguns grupos destas áreas. Tudo isso contribui para que o tema 'predadores e parasitas de aranhas' seja um campo muito promissor para trabalhos futuros, tanto para aracnólogos, quanto para todos os pesquisadores que trabalham com os demais grupos taxonômicos envolvidos nessas interações.

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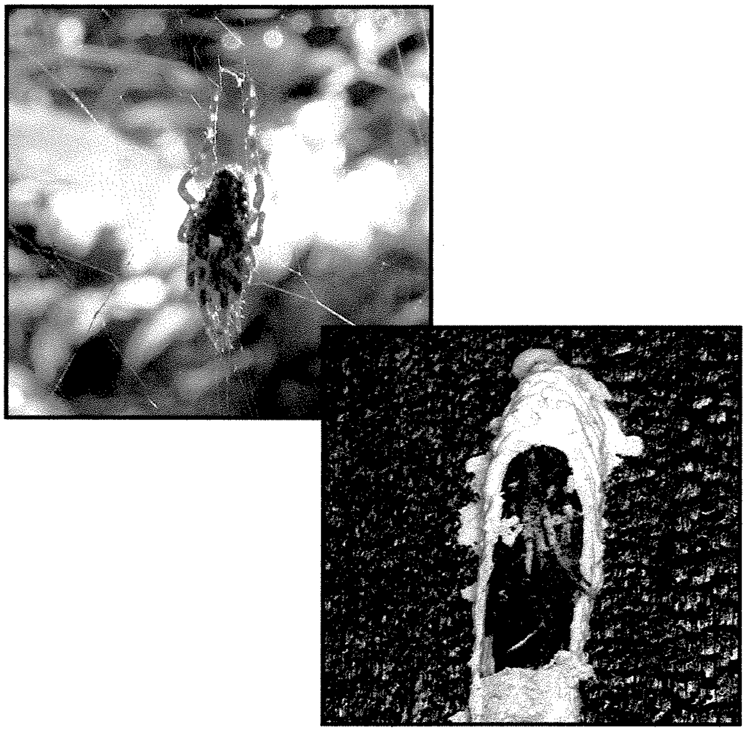
Capítulo 2

Orb-web spiders (Araneae: Araneomorphae; Orbiculariae) captured by hunting-wasps in two areas of Atlantic Forest in Southeastern Brazil.



ORB-WEB SPIDERS (ARANEAE: ARANEOMORPHAE; ORBICULARIAE) CAPTURED BY HUNTING-WASPS IN TWO AREAS OF ATLANTIC FOREST IN SOUTHEASTERN BRAZIL

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Running title: Orb-web spiders captured by wasps

ABSTRACT

Members of two hunting-wasp families, Pompilidae and Sphecidae, are among the major predators of orb-web spiders. In this study we collected paralyzed spiders from natural and trap-nests provisioned by hunting-wasps in two areas of the Brazilian Atlantic Forest, comparing these data with the composition of species collected by visual search during one year. Prey preferences were analyzed based on relative abundance of spider species, their size and web characteristics. We also compiled the lists of orb-weavers captured by four sphecid genera presented in 40 other studies. A large number of prey was obtained from natural nests of *Trypoxylon* (*Trypargilum*) *albonigrum* in Parque Estadual Intervales, especially species of *Eustala*, *Parawixia* and *Araneus* (Araneidae). Other prey, stored in trap-nests by *T. lactitarse* and unidentified species, include *Nephila* (Tetragnathidae), *Parawixia*, *Ocrepeira*, *Mecynogea*, *Acacesia* (Araneidae) and other species, less abundant. All the heavily preyed species had a relatively lower abundance in our samples of prey availability. In Floresta da Cicuta, most specimens were captured by a pompilid, *Auplopus argutus*, that hunts exclusively for cursorial species. Nests occupied by *T. lartitarse* in this area were provisioned mostly with *Parawixia* and *Araneus*. The range of body sizes of spiders captured by *Trypoxylon* in our study areas include the size of some abundant orb-weavers always absent in their nests. These results indicate that factors other than abundance in the field and spider's size are influencing prey selection or susceptibility to attacks.

Key-words: Sphecidae, Pompilidae, orb-web spiders, trap-nests, predation.

INTRODUCTION

All members of the wasp family Pompilidae and six genera of Sphecidae (*Trypoxylon*, *Chalybion*, *Sceliphron*, *Pison*, *Miscophus* and *Pisonopsis*) use exclusively spiders to provide food for their larvae (Blackledge *et al.* 2003, Bohart & Mencke 1976, Wasbauer 1995). Some parasitoid pompilids attack spiders within host refuges (usually cavities dug in the soil or shelters made of plant parts and silk). In these cases, spiders are not removed and transported to a nest, remaining paralyzed by wasp's venom in their own lairs. Other species attack wandering spiders, laying an egg on their bodies after inflicting just a temporary paralysis. When the effect of wasp's venom wears off, the spider is able to continue its normal activities until be serious injured by the larva attached to its body (Kaston 1959, O´Neill 2001). Most species, however, capture one spider and deposit this prey in a nest constructed with mud and attached to the surface of sheltered substrates, or in a nest created by the modification of a natural cavity or excavation of a new one (O´Neill 2001). All these three nesting habits can also be found in sphecids (Coville 1987, Hanson

& Menke 1995), and wasps of both families can be responsible for a significant impact on their prey populations (see Conley 1985, Laing 1988, McQueen 1978, Polis *et al.* 1998).

The main difference between Sphecidae and Pompilidae prey storage behaviors is the number of spiders stored for each larva. Sphecids store several small (relatively to their size) spiders in each cell of their nests, while pompilids supply their brood cells with a single large spider (Coville 1987, O'Neill 2001). Foraging efficiency using both strategies are constrained by the energy costs of transportation and by the time expended to find appropriated prey items. Pompilids must choose their prey size very carefully because the size and fecundity of their offspring will be correlated with the amount of nutrients contained in each specimen captured (Endo & Endo 1994, Rayor 1996). Sphecids, however, have a higher flexibility in relation to spider's size selection, being able of supplying the nutrients required for larva development depositing several small specimens. In spite of that, if the captured spiders were too small, the wasps will have to make more trips from the foraging area to the nesting sites, spending more energy and exposing their nests to parasites for a longer time.

In addition to spider's size and, of course, their availability in habitats exploited by the wasps, anti-predator devices can also be important to determine which species will be located and captured. Within the large range of defensive mechanisms that have evolved in spiders in response to predation (see Cloudsley-Thompson 1995), three-dimensional webs in Orbiculariae probably are among the most effective against capture attempts by hunting-wasps (Blackledge *et al.* 2003). Surrounding themselves with web threads, spiders can be benefited in two ways: the threads can directly block the approximation of wasps and transmit vibrations, warning their owners of an imminent attack (Uetz & Hieber 1994). Blackledge *et al.* (2003) compiled all the registers of spiders captured by sphecids published over the last century and compared this data set with the records of potential prey available in habitats from 26 faunal surveys. They concluded that the relative abundance of araneoid sheet web weavers found in wasp's nests is much lower than the expected based on their abundance in the field. In most studies, orb-weavers were captured in a higher frequency than spider species that build webs with a three-dimensional architecture. This argue forward the conclusion that two-dimensional orb-webs, in spite of their efficiency in retaining flying insects and their silk economy, are associated to a higher risk of predation by wasps. Modifications of this design to another one that includes additional protection may be the cause of the great diversification and abundance of araneoid sheet-weavers observed nowadays (Blackledge *et al.* 2003).

However, are all orb-weavers submitted to equally predation risks? A number of web characteristics and variations in orb-web spider's behavior and morphology suggests that the susceptibility to predation may be different among species. Spider's rest position (Herberstein & Heiling 2001) and escape behaviors (Blackledge & Picket 2000), the addition of web decorations (stabilimenta) (Blackledge & Wenzel 2001), spider's size (Camillo & Brescovit 1999a), body shape (Freeman & Johnston 1978) and thickness of integument (Elgar & Jebb 1999), presence and kinds of refuges (Eberhard 1970), and the establishment of aggregations (Alves-Costa & Gonzaga 2001, Henschel 1998, Uetz & Hieber 1994) are some factors that may interfere in location and capture success of orb-web spiders by wasps.

In this study we evaluated the species composition of orb-web spiders captured by wasps in two areas of Atlantic Forest, considering the relative abundance of these species in the field, their size and web characteristics. We also analyzed lists of orb-web spiders captured by sphecids published in 40 other studies on four sphecid genera (*Trypoxylon*, *Pison*, *Chalybion* and *Sceliphron*).

METHODS

Study sites

This study was developed in "ARIE Floresta da Cicuta", a small (131 ha) forest fragment located in Volta Redonda (22°31'S; 44°07'W), State of Rio de Janeiro, Brazil, and in Parque Estadual de Intervales (24°16'S; 48°25'W), a state park that is part of a large protected forest continuum (120,000 ha), also located in Southeastern Brazil, State of São Paulo. Both areas are composed by old second growth and primary forest. The climate is characterized by a relatively dry-cold season from May to October and a wet-warm season from November to April.

Spiders in wasp´s nests

Spiders captured by wasps were obtained by the placement of 301 trap-nests in each area and by the sampling of natural nests of *Trypoxylon (Trypargilum) albonigrum* Richards, 1934 (Sphecidae). Mud nests of *T. albonigrum* were found in the walls of two houses located close to the trails selected for the fixation of trap-nests in P.E. Intervales (Fig. 2.1). Although some females had constructed nests composed by more than one pipe tube, we collected just spiders provisioned in the last tube. This procedure was applied because in old tubes prey items generally were in poor conditions due to consumption by the larvae.

Trap-nests were composed by bamboo steams with one extremity closed by the nodal septum. The steams vary in internal diameter between 6.1 and 17.5 mm and all of them had about the same length of 150 mm. Groups of seven trap-nests were placed in plastic involucres and fixed in wood poles (Fig. 2.2). Forty three of these units were distributed in each area, following secondary trails and river margins. The distance between sample units within each trail was about 10 meters.

Traps were inspected once a month during one year in each area, from November 2001 to October 2002 in F. Cicuta, and from December 2001 to November 2002 in P.E. Intervales. Mud nests of *T. albonigrum* were collected at the same occasions. The inspections were performed using an otoscope to verify nest occupation. Occupied trap-nests were removed and replaced by others with approximately the same internal diameter. Spiders present in the nests were identified and measured to evaluate prey size preference and the biomass investment for each larva in dry and wet seasons. Some very damaged specimens (and the cells where they were found) were excluded from the analysis.

Voucher specimens of the sphecids were deposited in Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil. The pompilids were deposited in the collection of Panama University Museum, Panama, and the spiders in Instituto Butantan, São Paulo, Brazil.

Estimative of spider's weight

As we frequently found some spiders partially consumed by the wasp's larvae, we decided to calculate spider's weight, and later the biomass investment per provisioned cell, based on their body size. Specific models of length-weight relationship are available for many insect orders (Beaver & Baldwin 1975, Sample *et al.* 1993, Schoener 1980), but studies proposing equations for spiders are based on very small samples and did not specify how many and which species or higher taxonomic groups were analyzed (see Hódar 1996, Rogers *et al.* 1977). Thus, in order to obtain a better weight estimation, we calculated the length-weight relationship using just orb-web spiders captured by wasps during this study.

We measured the total body length (distance between the anterior margin of the carapace and the distal point of the abdomen) and dry weight of 5 adult females of 6 orb-weaver genera (one species per genus). The following species were used for this analysis: *Parawixia audax, Araneus venatrix, Wagneriana janeiro, Alpaida venilae, Eustala* sp. and *Mangora* sp. (Araneidae). Length was measured to the nearest 0.01mm using a dissecting microscope with an ocular micrometer, and weight was determined to the nearest 0.1mg after drying the specimens for 12 hours in a stove at 100°C. The analysis was performed with data transformed to logarithms to reduce heteroscedasticity and allow the conversion of a power equation ($W = aL^{b}$) in a linear regression ($\log W = \log a + b \log L$) (Schoener 1980, Zar 1996). The biomass investment in each cell was calculated by multiplying the number of spiders by their estimated weight, based on the obtained length-weight regression equation.

Prey availability

The relative abundance of potential prey for wasps was established by sampling the first 100 orb-web spiders located by visual search. This procedure was repeated every month during one year, at the same period of trap-nests inspections and the sample of mud nests of *T. albonigrum*. Spiders were collected along trails, in river margins and in forest interior, from the nesting sites until a distance of approximately 300 meters from them, always between 8:00 and 16:00. All the individuals, adults and juveniles, with webs placed up to about two meters from the ground were collected, conserved in ethanol 70% and transported to laboratory. All spiders were measured (total body length as described in the previous section) to compare the size distribution of available prey with spider's size in wasp's nests.

Some characteristics of webs, supposedly associated to predation avoidance, were registered for each species collected: presence of silk and detritus stabilimenta, refuges composed by silk and/or curled leaves, and barriers of silk threads. We also registered if each spider was resting at the hub of web or in the periphery, close to vegetation.

Prey lists from other studies

We compiled 40 studies, published from 1928 to 2002, presenting lists of orb-web spiders captured by sphecid wasps. As we were interested in prey preferences, studies involving very small samples (number of spiders collected < 10) were not considered. These include all the studies on the genus *Miscophus*, which capture mainly spiders with other kinds of webs (Blacklegde 2003), and *Pisonopsis*. For this last genus there is only one study available on prey selection, and from 41 spiders collected, only one was an orb-weaver (Evans 1969).

RESULTS

Spiders captured by wasps in Parque Estadual Intervales

Trap-nests

Twenty one trap-nests were provisioned by hunting-wasps in P.E. Intervales, but in 12 of them the larvae had already consumed all the spiders when we opened the traps. In the nine others we collected a total of 125 spiders, belonging to four families (Mimetidae, Tetragnathidae, Araneidae and Salticidae). All mimetids (20 individuals) were deposited in a single nest collected in January 2002, composed by six mud cells shaped as vessels. The other eight trap-nests containing spiders were divided in cells by mud plugs. All the 51 immature individuals of *Nephila clavipes* (Tetragnathidae) were collected in two nests, also in January. These nests also contained specimens of the araneids *Acacesia villalobosi*, *Araneus workmani*, *Mecynogea biggiba*, *Ocrepeira jacara*, *Parawixia audax*, *Eustala* sp.1 and *Eustala* sp.8. The unique specimen of Salticidae was collected in March, in a nest composed by three cells, two of which partially destructed and without any prey. We could not capture the female wasps or raise the larvae until they reach the adult stage to identify the species that constructed these nests. The remaining nests (another one from March and four from November), were provisioned by *Trypoxylon (Trypargilum) lactitarse* Saussure, 1867 and contained only species of Araneidae, especially *Parawixia audax* (41.6% of the total number of spiders captured by this wasp species) and *Eustala* spp. (30.5%) (Table 2.1, Fig. 2.3).

Trypoxylon lactitarse captured prey with body length varying from 3 to 10.4mm ($\overline{X}$ ± sd = 6.1 ± 2.0mm, n = 34 spiders). We did not calculate the biomass provisioned for each larva in *T. lactitarse* nests because many cells presented at least one spider almost entirely consumed. Furthermore, we obtained just five nests of this species and the results would be inconclusive. The orb-web spiders found in trap-nests provisioned by the unidentified species varied from 4.2 to 11.7mm of body length ($\overline{X}$ ± sd = 6.6 ± 1.7mm, n = 52 spiders).

Trypoxylon albonigrum mud nests

We collected the content of 69 individual nests of *Trypoxylon albonigrum*. The mean number of nests in contiguous positions was 2.4 ± 1.4 (varying from 1 to 6, n = 40) and the mean number of cells provisioned by each female was 8.7 ± 6.7 (varying from 2 to 30, n = 40 nests or nest aggregations). Although these numbers represent only nests with the entrance already closed, we can not be sure if each female had completed the egg laying process, and new nests could still be added to small aggregations or contiguous to individual nests.

A total of 702 orb-web spiders were present in the natural nests, most of them (91.3%) belonging to three genera, *Eustala* (65.1%), *Parawixia* (18.9%), and *Araneus* (7.3%). These genera represented more than 70% of all spiders collected by *T. albonigrum* in every month of this study (Fig. 2.4). However, they were rarely collected in prey availability surveys: *Eustala* (2.5%), *Parawixia* (0.8%) and *Araneus* (4.8%) (Table 2.1, Fig. 2.3). Furthermore, the most abundant species of *Araneus* captured by *T. albonigrum, A. uniformis*, was absent in our samples.

Prey body length in *T. albonigrum* nests varied from 1.5 to 11.8 mm ($\overline{X}$ ± sd = 6.5 ± 1.8mm, n = 700 spiders). This wide range include the body size of the most abundant spider species captured in prey availability surveys: *Cyclosa* (Araneidae), *Leucauge* (Tetragnathidae) and *Verrucosa* (Araneidae). However, their small juveniles (which represent most individuals in our samples) are in size categories rarely exploited by *T. albonigrum* (Fig. 2.5).

The overall proportion of adult spider females in *T. albonigrum* nests (42.3%) was similar to that of juveniles (44%). Adult males corresponded to only 1% of the prey items and 12.7% were subadult males. Most mature females were found in the end of the wet season, from February to May (Fig. 2.6).

Estimative of spider's weight

The regression between body length and dry weight was significant and presented a high value of r^2 (Fig. 2.7), allowing the estimative of the later variable based on the former. There is no significant difference between the biomass stored for each larva (Mann-Whitney U=470, p=0.421 n_1=38, n_2=28) or the number of spiders deposited per cell (Mann-Whitney U=487, p=0.332 n_1=39, n_2=29) of *T. albonigrum* nests in dry and wet seasons.

Web characteristics

Eustala webs can eventually be found during daytime, but generally are destructed or consumed in the morning, being rebuild every evening. Spiders rest in vegetation stems or leaves in a cryptic position (Fig. 2.8), making their location by visual inspection very difficult when webs are not present. All the five species of *Araneus* were found resting at the margin of their webs, in retreats made of web threads and curled up leaves. Some specimens of *A. venatrix* were seem leaving these shelters and capturing insects during the day. Both *Cyclosa* species build detritus stabilimenta, resting between two segments of these linear structures or, less often, in the extremity of the column (see Gonzaga & Vasconcellos-Neto in prep.). *Parawixia audax* and *P. velutina* were generally found in the hub of the webs, but eventually in rolled leaves outside the spiral zone. *Leucauge* spp. also remain exposed in their horizontal webs, running to the bridge threads after perceiving a threat.

Spiders captured by wasps in Floresta da Cicuta

Orb-web spiders in Floresta da Cicuta were found only in two nests constructed by *Trypoxylon lactitarse* females, one in November 2001 containing 25 spiders, and another in February 2002, with eight spiders. *Trypoxylon lactitarse* captured orb-weavers of two families in this area (Araneidae – genera *Parawixia, Araneus, Wagneriana, Mangora, Alpaida* and *Eustala*; and Tetragnathidae – *Crysometa*), and other Araneoidea that build very modified and inconspicuous kinds of webs (Uloboridae – *Myagramopes*; Deinopidae – *Deinopis*). Two cursorial specimens (corinids) were deposited in the nest collected in November. The most abundant spiders in prey availability survey were the araneids *Metazygia laticeps* (28.2%), *Araneus venatrix* (20.2%), *Cyclosa morretes* (13.7%) and *Cyclosa fililineata* (7.2%) (Fig. 2.9). From these, only *A. venatrix* was present in *T. lartitarse* nests.

All wandering spiders (families Salticidae, Sparassidae, Anyphaenidae, Ctenidae, and Corinidae) deposited in trap-nests were captured by *Auplopus* (Pompilidae), except the two specimens of Corinidae (labeled as CO1) captured by *T. lactitarse*. A high proportion of their prey (54.2%) was composed by adult spider females, 27.1% by juveniles and 18.8% by subadult males. This *Auplopus* species construct small mud vessels in the interior of trap-nests, depositing just one spider per vessel, generally with legs amputated. Females were identified, based on Dreisbach (1963) descriptions, as *Auplopus argutus*. Males, raised from the same trap-nests, were identified as *Auplopus pratensis*. Each one of these species is known only by a single sex, what suggests that they are conspecifics (Roberto Cambra T., personal communication).

Web characteristics

Metazygia laticeps remain in retreats during the day. Small juveniles always construct their webs close to a tendrill, where they hide themselves. Adults generally attach curled dry leaves to the bridge thread of their webs, remaining inside these refuges during the day. The webs of the other highly abundant species, *Araneus venatrix*, *Cyclosa* *morretes* and *Cyclosa fililineata* have the same general characteristics previously described for specimens collected in P.E. Intervales. The eight individuals of *Parawixia*, located during prey availability surveys, were seen resting unprotected during the day in the hub of their webs. Another prey of *T. lactitarse*, *Wagneriana janeiro*, assumes a cryptic position in dry branches and can be located by the researchers only through the presence of their thin vertical orb-webs.

Prey lists from other studies

Most sphecids capture a wide variety of orb-web spider genera. In spite of that, a maximum of 3 genera constitute more than 50% of the orb-weavers captured in each population of all species of *Chalybion, Pison, Sceliphron* and *Trypoxylon* included in the 41 studies analyzed (Table 2.2). In some species, as *T. monteverde* (Coville 1982) or *T. palliditarse* (Bruch 1930), all spiders collected belong to a single genera. In many others just one or two genera represent more than 80% of all orb-weavers deposited in the nests (see Matthews 1983, Muma & Jeffers 1945, Cross *et al.* 1975). *Eustala*, *Araneus* and *Neoscona* appear in many lists among the most abundant prey. Others, as *Cyclosa* and *Verrucosa*, were absent or present in low abundance in prey lists for most wasps species, but were heavily captured for at least one of them.

DISCUSSION

The composition of species and abundance of the spiders collected by wasps were very distinct from the obtained by the visual search method on both study areas. These results suggest that wasps are extremely selective, preying on relatively rare species. The estimative of prey availability for wasps, however, involve some problems that must be analyzed carefully. First, foraging habits of most wasp species are unknown and some can capture their prey in places usually not inspected by the researchers. Roble (1985), for example, studied the hunting behavior of the pompilid *Anoplius depressipes* and showed that it captures the spider *Dolomedes triton* (Pisauridae) under water. Besides, prey availability surveys generally do not include the higher strata of vegetation and the relative abundance of each spider species in these places can be different from the abundance in the lower bushes and herbaceous stratum (Silva 1996, Sørensen 2003), which are usually inspected.

Even considering just the usual sampled places, we can not be sure about the extension of the hunting area used by the wasps, and spider distribution can vary in space according to density of vegetation, microclimatic conditions, and prey availability (Enders 1972, Ward & Lubin 1993). This problem, however, is minimized by the fact that hunting-wasp species must reduce the distance between the nesting area and foraging sites to as minimal as possible, in order to reduce the amount of time and energy expended during nest provisioning, the risks of having the prey stolen by another wasp or other insects, and parasitism by flies. The distance between nesting sites and the hunting area is usually unknown for wasps, but observations on the sphecid genera *Tachytes* (Kurczewski & Spofford 1986), *Podalonia* (O'Brien & Kurczewski 1982), and *Aphilanthops* (O'Neill 1994), for example, suggest that it is restricted to a few meters. We collected spiders around the area where we placed the trap-nests and around the two houses where we collected the natural nests of *T. albonigrum*, but at least part of the difference between the lists of prey collected by wasps and by ourselves may be explained by differences in the sampled sites.

The next problem is that any sample method is more effective for some spider species or species groups than for others (Scharff 2003, Sørensen *et al.* 2002). Sweeping the lower herb layer with a net or beating branches to catch the falling spiders, for example, may include specimens that actually are not available because they are resting inside their refuges. They may be safe in these places because sphecids are generally unable to pursue spiders into confined spaces (Coville 1987 - but see Blackledge & Pickett 2000 for an example of an alternative strategy employed by wasps to capture spiders in retreats). Furthermore, staying in these refuges, spiders are less conspicuous to their predators. The visual search method, on the other hand, probably underestimate the abundance of species that construct webs only at night, but can be located and captured by wasps while resting relatively unprotected on vegetation during the day. This is the case of *Eustala*, the main prey item in *T. abonigrum* nests and also in nests of many other sphecids (see Table 2.2). As they consume the webs by the morning, the main visual sign that usually attracts our attention to the spiders are not available. Sphecids, however, can use many techniques to locate spiders: alighting on bumps and spots, tapping surfaces with the antennae, and examining webs and attracting spiders by pulling and vibrating web threads (Coville 1987, Laing 1988). By the visual search method we are able to locate webs and conspicuous spiders, but the relative abundance of cryptic spiders that can be touched by wasps during tactile inspections probably is underestimated.

Finally, insect vision is very distinct from human vision in several aspects. Color differentiation in insects, for example, is made fundamentally by contrast, while we distinguish colors through differences in brightness (Backhaus 1991, Lunau *et al.* 1996). Our eye resolution is also much better and we can identify a spider web from a distance substantially higher than any insect is able to do. In addition, objects that reflect white plus UV-light are perceived by insects as having the same color of the background composed by leaves or soil (Blackledge 1998). We perceive these objects as white because we are able to see red light wavelengths, while very few insects are sensitive to red (Briscoe & Chittka 2001). Therefore, some spider species that construct very conspicuous webs and/or have bright colors perceived by our eyes, may be located by wasps in a lower frequency. This may be the case of the *Cyclosa* species collected in abundance during prey availability surveys on our both study areas. The researchers, even involuntarily, used the visual sign of the stabilimenta to locate the otherwise inconspicuous *Cyclosa* webs. The shape and color pattern of the detritus column (the most common type of stabilimentum of *C. morretes* and *C. fililineata*), however, may be overlooked by predators searching for spiders (see Gonzaga & Vasconcellos-Neto, in prep.).

All these limitations restrict our capacity to evaluate prey availability for wasps. But the comparison between samples conducted by human and wasps are useful to indicate which kinds of potential prey are being avoided or not located by these predators. This is important to access the effectiveness of different kinds of anti-predator strategies observed in spiders. Prior to analyze that aspect, however, it is necessary to account prey size preferences. Some spider species or individuals in specific maturation stages can be avoided by wasps simply because represent packets too small to feed the larvae or too heavy to be transported. Furthermore, the relation between wasp and spider sizes can be an important variable influencing the success of predatory attacks and, in fact, a positive correlation between female size and their prey size has been described for many species of solitary wasps (O'Neill 1985, Gwynne & Dodson 1983). Our results indicate that *T. albonigrum and T. lactitarse* use a wide range of prey sizes. The most abundant genera of orb-web spiders collected in our prey availability surveys in P.E. Intervales (*Cyclosa, Leucauge* and *Verrucosa*) presented body sizes included in this range. Adult females of *Cyclosa fililineata*, *C. morretes*, *Leucauge* spp., and some subadult and adult *Verrucosa* are in the same size categories of most prey captured by *T. albonigrum*. In spite of that, these potential prey were always absent in their mud nests, as well as in the trap-nests provisioned by the other wasp species in P.E. Intervales. This indicate that foraging behavior of wasps is not determined just by the selection for spider prey of specific sizes.

It is interesting to note that two of the most abundant spider genera collected by *T. albonigrum* and *T. lactitarse* in P.E. Intervales, *Eustala* and *Araneus*, usually stay outside their webs during the day. *Araneus* is often found hidden in retreats. The other highly frequent species, belonging to the genus *Parawixia*, remain exposed at the hub of their webs or, more often, relatively hidden close to vegetation. On the other hand, both *Cyclosa* species and *Verrucosa arenata*, absent in the wasp's nests, stay exposed in their orb-webs during the day. But both construct stabilimenta (the later composed only by silk). This indicate that the retreats composed by leaves and silk are not completely effective in protect these spiders against sphecids. It is possible, however, that silk and detritus stabilimenta may reduce the risk of predation. This last hypothesis is supported by empirical data on the araneid genus *Argiope*. Blackledge & Wenzel (2001) showed that wasps (*Chalybion caeruelum*) were 36% more likely to capture individuals of *Argiope trifasciata* that had not included stabilimenta in their webs, and argue that the linear silk stabilimenta built by this species could distract wasps during the attacks.

Web characteristics may also be an indicative of searching and attacking methods used by wasps. The presence of *Araneus venatrix* and *A. workmani* in the nests of *T. lactitarse* collected in Floresta Cicuta, for example, indicates that this wasp species probably is capable to locate spiders searching for their webs (once spiders remain hidden during the day), and remove them from the retreats. Capture techniques of some other sphecids include attracting spiders, vibrating their webs in order to simulate a intercepted prey (aggressive mimicry), and hitting the web to capture the resident spider when it jumps (Blacklegde & Pickett 2000, Laing 1988). It is possible that both strategies may be effective to capture these *Araneus* species.

Data regarding web types constructed by most species listed as preferential prey for hunting-wasps are not available. However, the webs of some spider species in genera heavily preyed by many wasp species were well described. *Neoscona arabesca*, for example, rests in the center of its vertical web during the night and stays in a retreat (usually a curled up leaf) during the day (Berman & Levi 1971). This species is very abundant in many locations of United States and Canada (Berman & Levi 1971) and was found in nests of *Trypoxylon* and *Sceliphron* species (e.g. Dorris 1970, Medler 1967, Volkova *et al.* 1999 - see Table 2). Many species of *Eustala* rest in shrubs or dead twigs during the day and make their webs in the evening (Levi 1977). This is the case of *E. anastera* (see Levi 1977 for web description), prey of *T. politum* (Muma & Jeffers 1945), *T. striatum* (Medler 1967), and *S. caementarium* (Branson 1966). The high proportion of these genera in nests of many wasp species indicate that the protection provided by their defensive devices are not completely effective against these predators. Some important information necessary to access this problem, however, are not available in most previous studies. Data on the relative abundance of species/genus that construct retreats, stabilimenta or that stay close to vegetation in cryptic positions during the day, associated with their frequency in wasp's nests, should be evaluated in other cases. It's also important to reduce the great geographical bias in these studies, including the large and comparatively almost unknown diversity of the Neotropical species, for example.

Another usually neglected aspect of prey selection is the proportion of each sex and the maturation stages of the spiders collected. The reduced number of adult and subadult spider males in the natural nests of *T. albonigrum* and in our trap-nests was also observed for other *Trypoxylon* species (e.g. Rehnberg 1987, Genaro & Alayón 1994). This pattern may be a consequence of a relatively lower capacity of wasps to locate individuals moving on vegetation. Adult araneid males leave their webs in order to search for females, reducing their exposition to predators that may use the web as a visual sign for approximation. Another possibility is that males can be avoided because they have a poor nutritional value. Rehnberg (1987) measured the lipid content of cells provisioned by *Trypoxylon politum,* showing that those with adult females were richer than others that include juveniles, and subadult and adult males. In addition, males of many araneids present a relatively smaller body size than females (see Hormiga *et al.* 2000). The proportion of juveniles and females in the nests may depend on the phenology of the preferential prey species. Adult females probably constitute a richer nutritional packet, due to the accumulation of fat tissue involved in egg production. However, the ability of wasps to discriminate between maturation stages is unknown.

The knowledge about foraging habits and prey preferences in pompilids is also an open area for future researches. The biology of many genera (e.g. *Mystagenia*, *Aplochares*, *Atopagenia*, *Balboana*, *Xenopompilus*) remains ignored (Wasbauer 1995). Even the relatively more studied genera, as *Auplopus*, still present many taxonomic problems and ecological data are available for few species. Although species in many genera of Pompilidae capture orb-web spiders (e.g. *Anoplius*, *Batazonellus*, *Episyron*, *Poecilopompilus* - see Kurczewski & Kurczewski 1968, Martins 1991, Rayor 1996, Wasbauer 1995), the genus *Auplopus* apparently capture exclusively spiders that forage on the vegetation or on the ground. Previous records of their prey include spiders of the families Anyphaenidae, Clubionidae, Ctenidae, Sparassidae, Philodromidae, Pisauridae, Salticidae and Thomisidae (Cambra *et al.* in press, Kurczewski & Kurczewski 1968, Wasbauer 1995). Prey items found in the nests of *Auplopus argutus* in Floresta da Cicuta showed that this species follows the same foraging pattern described for the genus, including a wide range of cursorial spiders, but no orb-weaver.

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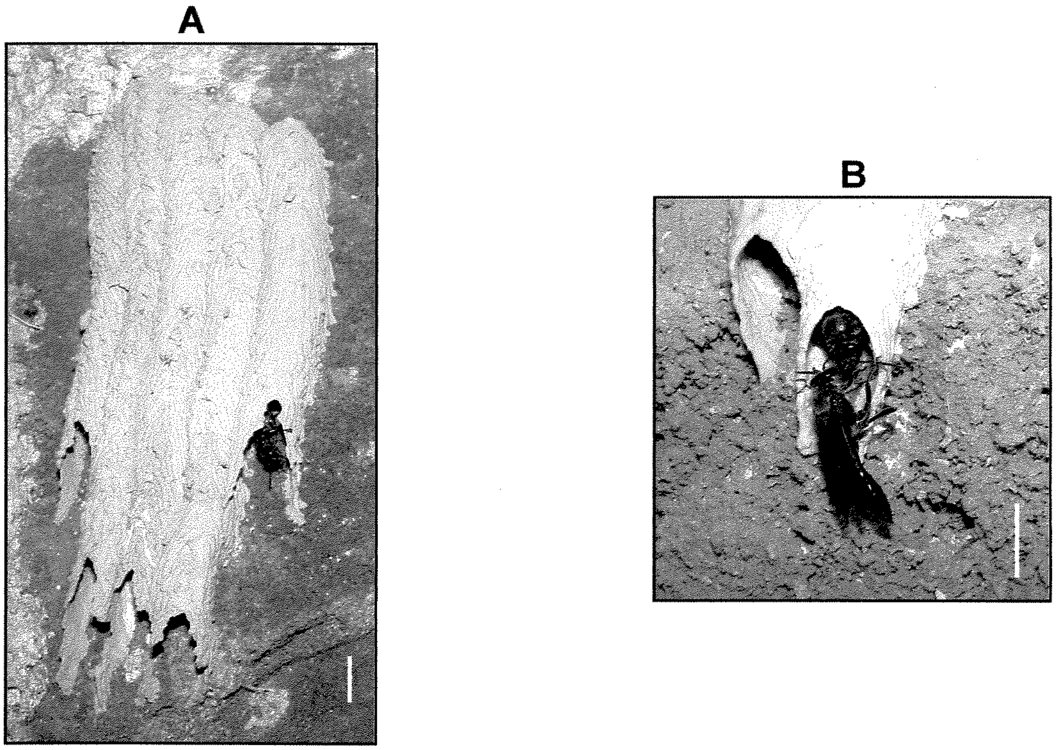

Fig. 2.1: (A) *Trypoxylon albonigrum* nests, (B) Female arriving at the nest site after collect mud. The male keeps guarding the nest entrance while she's hunting or colleting mud. Scales: 1cm.

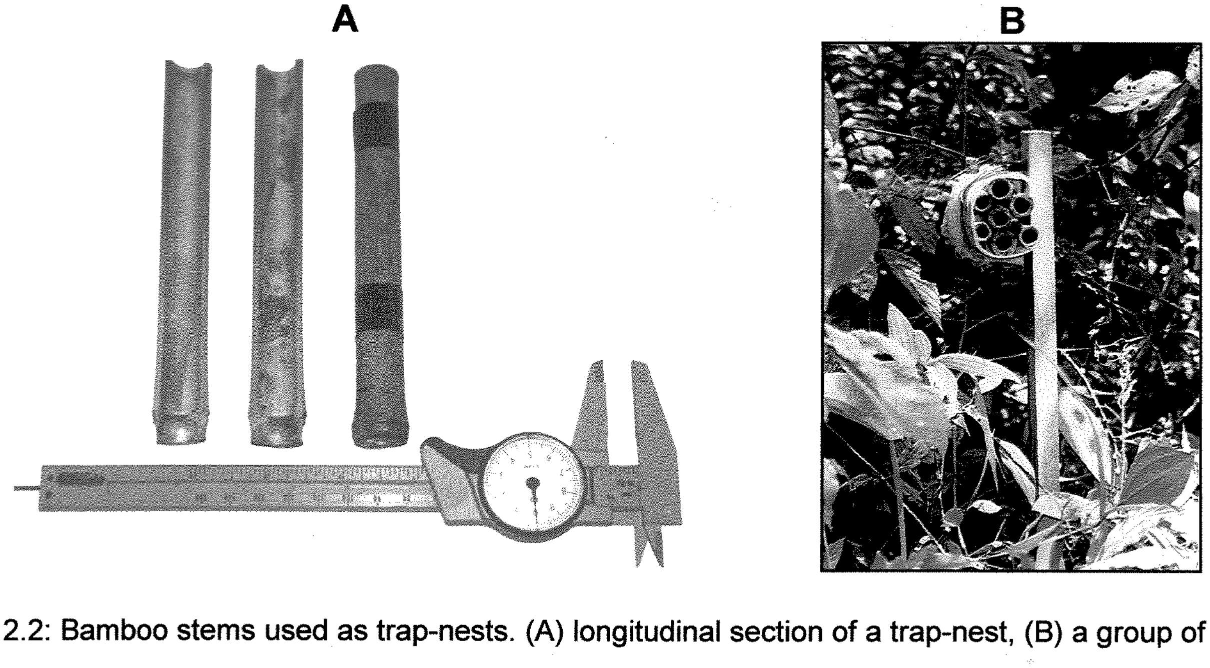

Fig. 2.2: Bamboo stems used as trap-nests. (A) longitudinal section of a trap-nest, (B) a group of seven trap-nests in the field.

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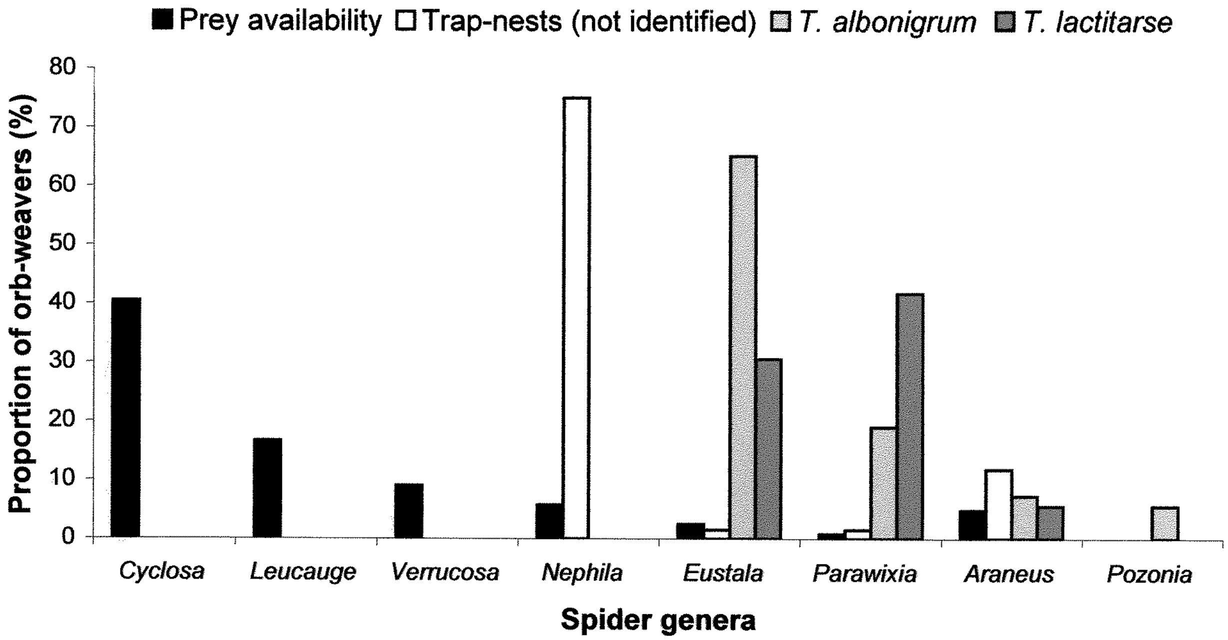


Fig. 2.3: Relative abundance of orb-weaver genera collected in trap-nests by unidentified wasp(s species, *Trypoxylon albonigrum, T. lactitarse* and by visual search in P.E. Intervales.

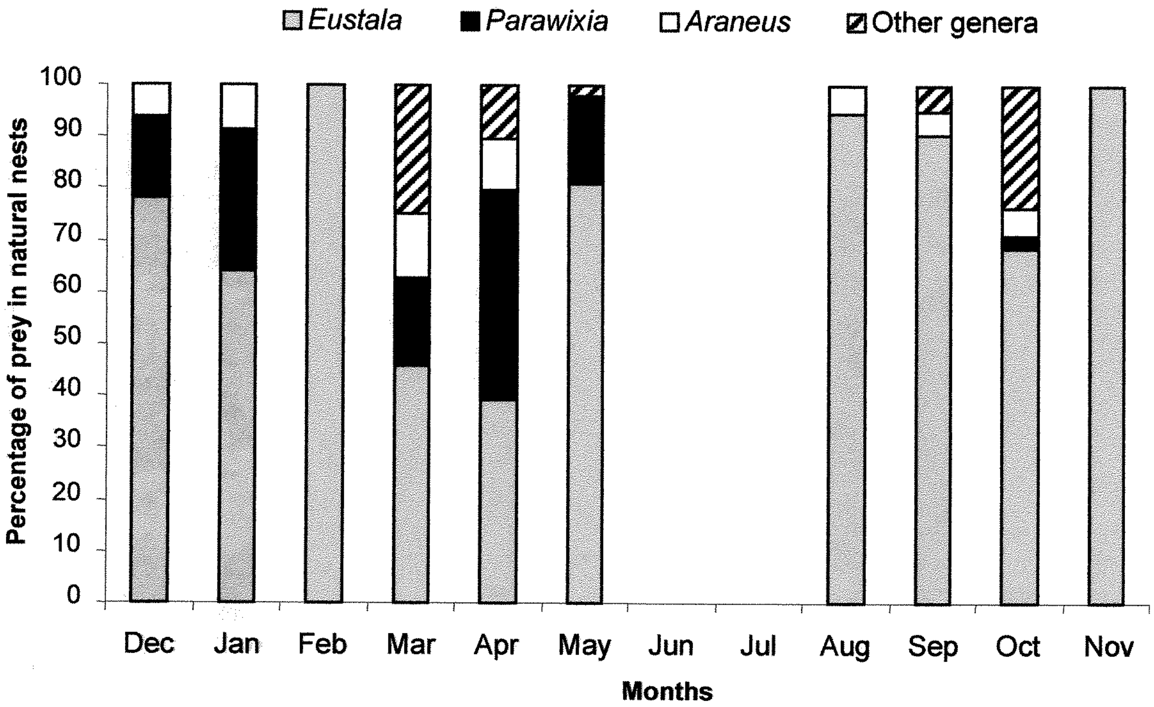


Fig. 2.4: Relative abundance of the three most common spider genera in *T. albonigrum* nests.

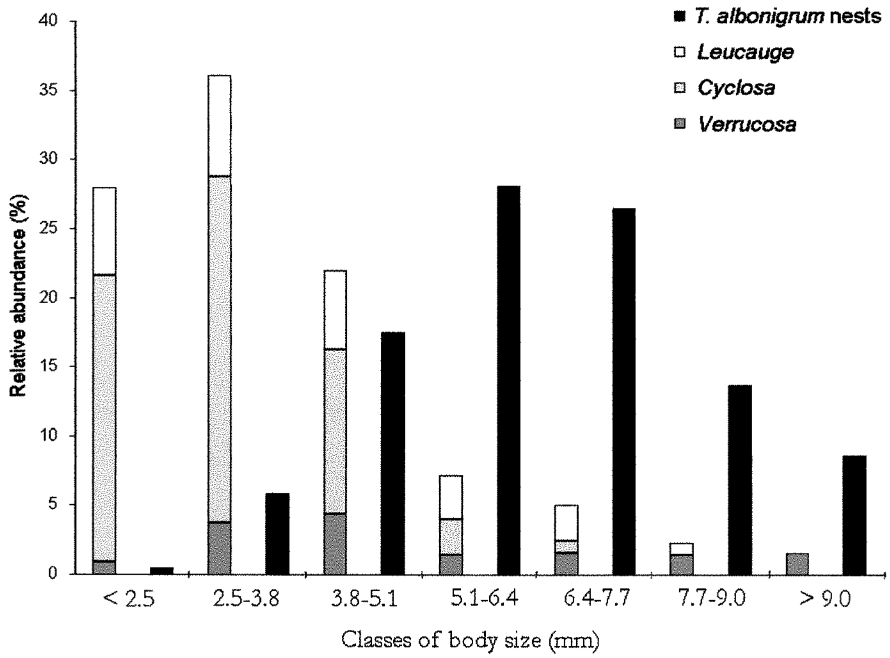


Fig. 2.5: Comparison between size distribution of spiders collected in *T. albonigrum* nests with spiders belonging to the three most abundant genera in prey availability surveys.

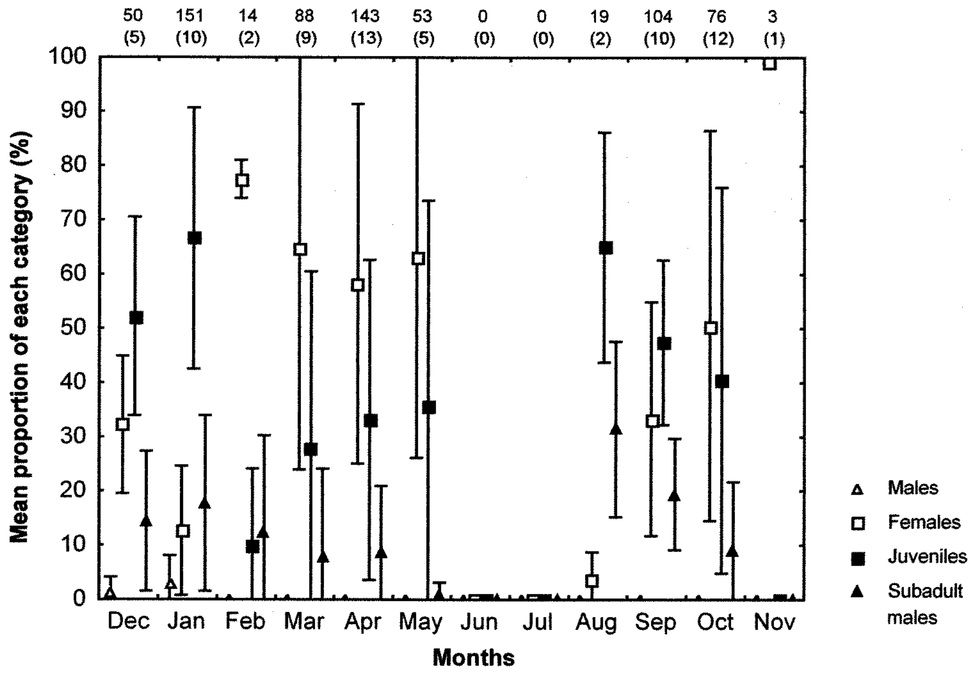


Fig. 2.6: Proportion of adult spider males, adult females, juveniles and subadult males in *T. albonigrum* nests, during the year. The numbers above the graphic indicate the number of spiders collected in each month and, in parenthesis, the number of nests.

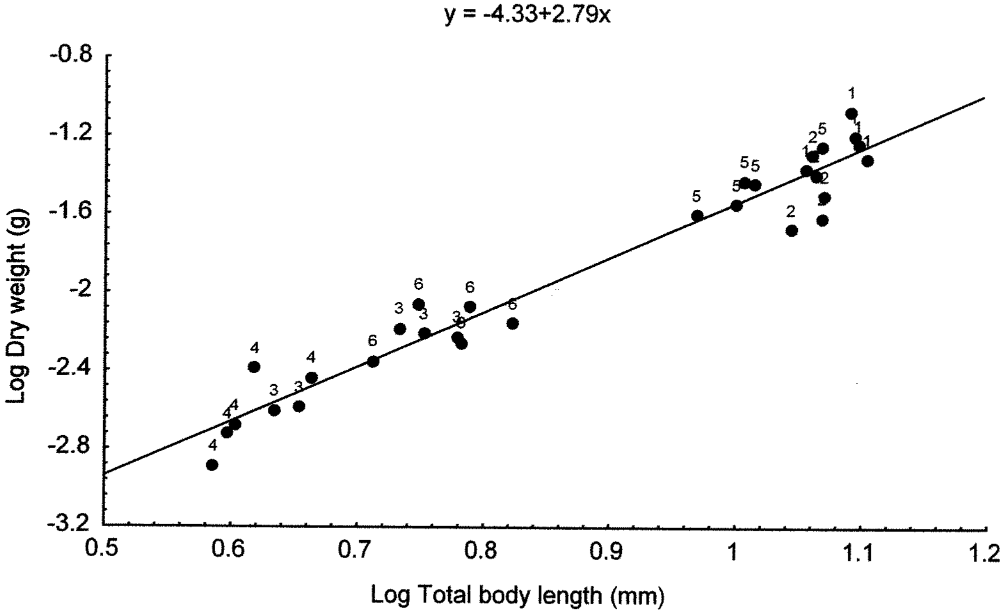


Fig. 2.7: Regression between body length and dry weight of six spider genera captured by *Trypoxylon albonigrum* and/or *T. lactitarse* (r^2=0.951, p<0.001, n=30). (1) *Araneus*, (2) *Alpaida*, (3) *Wagneriana*, (4) *Mangora*, (5) *Parawixia*, (6) *Eustala*.

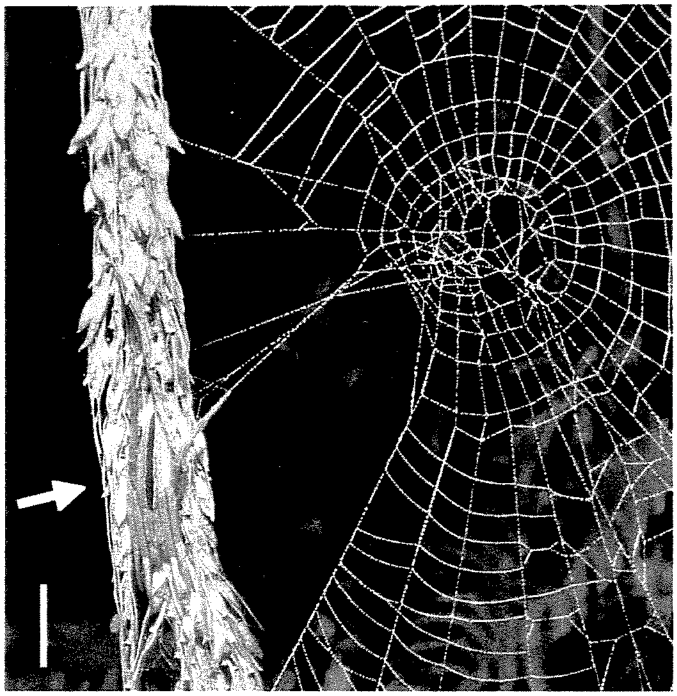


Fig. 2.8: *Eustala* sp.8 resting on vegetation. The spider remains holding a thread connected with the web hub. Scale: 1cm.

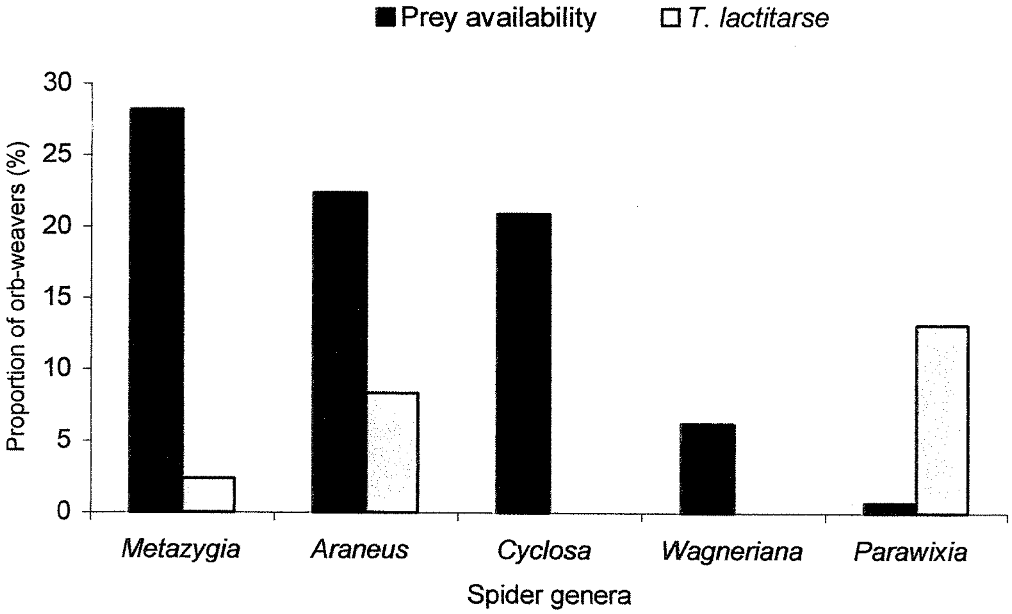


Fig. 2.9: Relative abundance of orb-weaver genera collected in trap-nests by *Trypoxylon lactitarse* and by visual search in F. Cicuta.

Table 2.1: Number of specimens collected in the periods from November 2001 to October 2002 in Flores da Cicuta and December 2001 to November 2002 in Parque Estadual Intervales. (* - see "Anexo 1", ** - se "Anexo 2", ? - species not indentified).

	Prey availability		**Trap-nests**				**Natural nes**
	Cicuta	Intervales	Cicuta		Intervales		Intervales
Species			*A. argutus*	*T. lactitarse*	?	*T. lactitarse*	*T. albonigru*
Araneidae							
Acacesia sp.1	0	0	0	1	0	3	0
Acacesia villabosi	0	1	0	0	1	0	0
Alpaida canoa	1	0	0	0	0	0	0
Alpaida caxias	0	0	0	1	0	0	0
Alpaida veniliae	0	21	0	0	0	4	0
Alpaida truncata	0	1	0	0	0	0	0
Alpaida sp.1	1	0	0	0	0	0	0
Araneus bogotensis	3	5	0	0	0	1	1
Araneus corporosus	0	6	0	0	0	0	1
Araneus uniformis	0	0	0	0	0	0	47
Araneus venatrix	227	38	0	5	0	0	0
Araneus vincibilis	11	2	0	0	0	0	0
Araneus workmani	10	7	0	2	8	1	1
Araneus sp.1	0	0	0	0	0	0	1
Argiope argentata	6	24	0	0	0	0	0
Bertrana rufostriata	0	0	0	0	0	1	0
Cyclosa bifurcata	0	2	0	0	0	0	0
Cyclosa fililineata	81	392	0	0	0	0	0
Cyclosa morretes	154	92	0	0	0	0	0
Eriophora sp.	15	0	0	0	0	0	0
Eustala sp.1	0	0	0	0	1	1	5
Eustala sp.2	0	0	0	1	0	0	6
Eustala sp.3	0	0	0	0	0	1	167
Eustala sp.4	0	12	0	0	0	6	124
Eustala sp.5	0	6	0	0	0	0	0
Eustala sp.6	0	0	0	1	0	0	16
Eustala sp.7	0	0	0	0	0	0	8
Eustala sp.8	0	9	0	0	0	2	96
Eustala sp.9	0	0	0	0	0	0	7
Eustala sp.10	0	0	0	0	0	0	4
Eustala sp.11	0	0	0	0	0	0	1
Eustala sp.12	0	0	0	0	0	0	2
Eustala sp.13	0	0	0	0	0	0	6
Eustala sp.14	0	0	0	0	0	1	5
Eustala sp.15	0	0	0	0	0	0	3
Eustala sp.16	0	0	0	0	0	0	3
Eustala sp.17	1	0	0	0	0	0	0
Eustala sp.18	0	3	0	0	0	0	0
Eustala sp.19	0	0	0	0	0	0	2
Eustala sp.20	0	0	0	0	0	0	2
Gasteracantha cancriformes	0	14	0	0	0	0	0
Hypognatha sp.	0	5	0	0	0	0	0
Kapogea sellata	12	0	0	0	0	0	0
Mangora sp.1	11	14	0	0	0	0	0

	Prey availability		Trap-nests				Natural nests
	Cicuta	Intervales	Cicuta		Intervales		Intervales
Species			*A. argutus*	*T. lactitarse*	?	*T. lactitarse*	*T. albonigrum*
Mangora sp.2	7	17	0	1	0	0	0
Mangora sp.3	0	18	0	0	0	0	0
Mangora sp.4	1	0	0	0	0	0	0
Mangora sp.5	5	1	0	0	0	0	0
Mangora sp.6	0	0	0	0	0	0	21
Mecynogea biggiba	0	4	0	0	5	0	0
Metazygia laticeps	317	0	0	0	0	0	0
Metepeira sp.1	0	3	0	0	0	0	0
Micrathena crassispina	10	9	0	0	0	0	0
Micrathena digitata	0	1	0	0	0	0	0
Micrathena fissispina	0	15	0	0	0	0	0
Micrathena guanabara	29	4	0	0	0	0	0
Micrathena horrida	3	0	0	0	0	0	0
Micrathena jundiai	7	6	0	0	0	0	0
Micrathena plana	0	12	0	0	0	0	0
Micrathena sp. (new species)*	1	0	0	0	0	0	0
Micrathena spitzi	1	10	0	0	0	0	0
Micrathena triangularis	2	2	0	0	0	0	0
Micrepeira sp.1	2	0	0	0	0	0	0
Ocrepeira jacara	0	0	0	0	1	0	0
Parawixia audax	4	8	0	0	1	15	133
Parawixia velutina	4	2	0	11	0	0	0
Pozonia bacillifera	0	0	0	0	0	0	39
Verrucosa arenata	1	108	0	0	0	0	0
Wagneriana eupalaestris	0	1	0	0	0	0	0
Wagneriana gavensis	2	0	0	0	0	0	1
Wagneriana jacaza	1	0	0	0	0	0	0
Wagneriana janeiro	67	0	0	2	0	0	0
Uloboridae							
Philoponella sp.1	0	8	0	0	0	0	0
Philoponella sp.2	26	25	0	0	0	0	0
Philoponella sp.3	1	0	0	0	0	0	0
Miagrammopes sp.1	1	2	0	1	0	0	0
Miagrammopes sp.2	0	0	0	1	0	0	0
Miagrammopes sp.3	0	1	0	0	0	0	0
Sybota sp. (new species)**	2	0	0	0	0	0	0
Zosis sp.1	0	2	0	0	0	0	0
Theridiossomatidae							
Naatlo sp.1	1	9	0	0	0	0	0
TH2	0	5	0	0	0	0	0
Tetragnathidae							
Azilia sp.	3	0	0	0	0	0	0
Crysometa sp.1	4	1	0	2	0	0	0
Crysometa sp.2	5	0	0	0	0	0	0
Leucauge sp.1	0	43	0	0	0	0	0
Leucauge sp.2	0	4	0	0	0	0	0
Leucauge sp.3	0	52	0	0	0	0	0

	Prey availability		Trap-nests				Natural nest
	Cicuta	Intervales	Cicuta		Intervales		Intervales
Species			*A. argutus*	*T. lactitarse*	?	*T. lactitarse*	*T. albonigru*
Leucauge sp.4	20	8	0	0	0	0	0
Leucauge sp.5	0	92	0	0	0	0	0
Leucauge sp.6	3	0	0	0	0	0	0
Nephila clavipes	37	69	0	0	51	0	0
Tetragnatha sp.1	26	0	0	0	0	0	0
Tetragnatha sp.2	0	1	0	0	0	0	0
Salticidae							
SA1	0	0	3	0	0	0	0
Psecas sp.1	0	0	1	0	0	0	0
Thiodina sp.1	0	0	1	0	0	0	0
Lyssomanes sp.1	0	0	1	0	0	0	0
SA5	0	0	0	0	1	0	0
Sparassidae							
SP1	0	0	1	0	0	0	0
SP2	0	0	6	0	0	0	0
SP3	0	0	2	0	0	0	0
SP4	0	0	1	0	0	0	0
Anyphaenidae							
Aysha sp.1	0	0	2	0	0	0	0
Aysha sp.2	0	0	1	0	0	0	0
Patrera sp.1	0	0	2	0	0	0	0
Anyphaenoides sp.1	0	0	2	0	0	0	0
Anyphaenoides clavipes	0	0	1	0	0	0	0
Teudis sp.1	0	0	2	0	0	0	0
Ctenidae							
Enoploctenus sp.1	0	0	1	0	0	0	0
Corinidae							
CO1	0	0	2	2	0	0	0
Corina sp.1	0	0	5	0	0	0	0
CO2	0	0	16	0	0	0	0
CO3	0	0	1	0	0	0	0
Mimetidae							
Gelanor sp.1	0	0	0	0	12	0	0
Gelanor sp.2	0	0	0	0	8	0	0
Deinopidae							
Deinopis sp.1	0	0	0	2	0	0	0
Total	**1126**	**1197**	**51**	**33**	**89**	**36**	**702**

Table 2.2: Main prey of four sphecid genera. In all 38 studies analysed including lists of orb-weavers captured by sphecids, more than 50% of prey items were represented by a maximum of 3 genera. These genera of preferential prey are presented here for each wasp species or population. 1-Asís *et al*. (1994); 2-Barber & Matthews (1979); 3-Branson (1966); 4-Bruch (1930); 5-Camillo (2002); 6-Camillo (1999); 7-Camillo & Brescovit (1999a); 8-Camillo & Brescovit (1999b); 9-Camillo *et al*. (1993); 10-Camillo *et al*. (1994); 11-Coville (1979); 12-Coville (1982); 13-Coville (1986); 14-Coville & Coville (1980); 15-Coville et al. (2000); 16-Cross et al. (1975); 17-Danks (1970); 18-Dorris (1970); 19-Edmunds (1990); 20-Elgar & Jebb (1999); 21- Genaro (1996); 22-Genaro & Alayon (1994); 23-Genaro *et al*. (1989); 24-Gonzales-Bustamante (1994); 25-Hook (1984); 26-Horner & Klein (1979); 27-Jiménez & Tejas (1994); 28-Jiménez *et al*. (1992); 29-Krombein (1970); 30-Laing (1988); 31-Lin (1969); 32-Matthews (1983); 33-Medler (1967); 34-Muma & Jeffers (1945); 35-O'Brien (1982); 36-Rau (1928); 37-Rau (1944); 38-Rehnberg (1987); 39-Ward (1970); 40-Volkova *et al*. 1999; 41-Present study. (*) This study presen

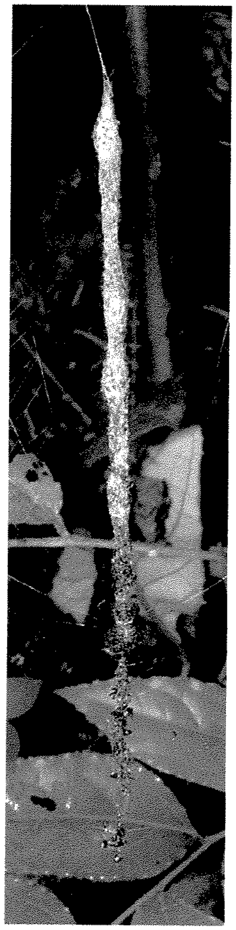
Wasp species	Spider genera (% of total orb-weavers)																									n (most abundant genera)	% of total orb-weavers	% of total spiders
	Eustala	*Araneus*	*Neoscona*	*Argiope*	*Alpaida*	*Parawixia*	*Acanthepeira*	*Pararaneus*	*Micrathena*	*Gasteracantha*	*Larinia*	*Eriophora*	*Dolichognatha*	*Gasteracantha*	*Singa*	*Metepeira*	*Metazygia*	*Mangora*	*Uloborus*	*Plesiometa*	*Tetragnatha*	*Araniella*	*Verrucosa*	*Cyclosa*	*Acacesia*			
Chalybion																												
[26]*C. californicum*	37.5						22.8																			88	60.3	42.0
[33]*C. coeruelum*		45.8	24.1																							174	69.9	18.8
[19]*C. fuscipenne*		9.9						70.0																		162	79.9	50.0
[38]*C. zimmermanni*		50.0		45.8																						23	95.8	57.5
Pison																												
[30]*P. morosum*		100																								12	100	46.2
Sceliphron																												
[03]*S. caementarium*	42.4			36.0																						359	78.4	62.3
[34]*S. caementarium*		42.1	49.2																							978	91.3	48.4
[21]*S. caementarium*	61.4																								31.8	82	93.2	91.1
[26]*S. caementarium*	55.7	23.5																								175	79.2	23.5
[40]*S. caementarium*			60.6	8.6																						2115	69.2	61.0
[05]*S. fistularium*					100																					57	100	100
[05]*S. fistularium*									85.9																	122	85.9	85.9
[28]*S. jamaincense*	20.2										17.3	16.3														56	53.8	7.8
[20]*S. laetum*			41.1	24.0						24.0																230	89.1	88.2
[18]*Sceliphron* sp.			18.7																17.3						20.4	241	56.4	25.4
[24]*Sceliphron* sp.									92.3																	385	92.3	92.3
[19]*S. spirifex*		45.7						17.4																		29	63.1	15.1

cont. **Wasp species**	Spider genera (% of total orb-weavers)																											
	Eustala	*Araneus*	*Neoscona*	*Argiope*	*Alpaida*	*Parawixia*	*Acanthepeira*	*Pararaneus*	*Micrathena*	*Gasteracantha*	*Larinia*	*Eriophora*	*Dolichognatha*	*Gasteracantha*	*Singa*	*Metepeira*	*Metazygia*	*Mangora*	*Uloborus*	*Plesiometa*	*Tetragnatha*	*Araniella*	*Verrucosa*	*Cyclosa*	*Acacesia*	**n (most abundant genera)**	**% of total orb-weavers**	**% of total**
Trypoxylon																												
^{41}*T. albonigrum*	65.1					18.9																				590	84.0	84.0
^{06}*T. antropovi*						25.0						63.9														32	88.9	88.9
^{34}*T. clavatum*				53.3																						387	92.6	88.2
^{36}*T. clavatum*	100																									10	100	10.8
^{29}*T. collinum*			100																							18	100	100
^{17}*T. figulus*															77.9											162	77.9	77.9
^{09}*T. lactitarse*	18.4				23.7	14.9																				65	57.0	53.7
^{07}*T. lactitarse*	35.1																								21.1	104	56.2	54.7
^{07}*T. lactitarse*	64.3					19.2																				548	83.5	81.9
^{07}*T. lactitarse*	27.4					17.3																			16.2	218	60.9	57.0
^{32}*T. latro*													95.5													127	95.5	95.5
^{12}*T. monteverde*	100																									31	100	100
^{12}*T. occidentalis*		50.0														47.1										33	97.1	97.1
^{11}*T. orizabense*		26.9*														26.9*										58	53.7	50.9
^{04}*T. palliditarse*		100																								39	100	100
^{02}*T. politum*			98.0																							49	98.0	98.0
^{34}*T. politum*	24.9		67.7																							387	92.6	23.7
^{37}*T. politum*			86.2																							25	86.2	86.2
^{31}*T. politum*	16.7		83.3																							36	100	100
^{38}*T. politum*		28.9	62.2																							722	91.1	91.1
^{40}*T. politum*	24.6		64.9																							830	89.5	88.1
^{08}*T. rogenhoferi*					76.5																					692	76.5	76.0
^{10}*T. rogenhoferi*					97.8																					178	97.8	97.3
^{08}*T. rogenhoferi*					93.3																					461	93.3	92.9
^{33}*T. rubrocinctum*																		56.3								27	56.3	20.5
^{18}*Trypoxylon* sp.	24.4		31.9																							240	56.3	25.3
^{31}*T. spinosum*			22.2																55.6							7	77.8	14.0

cont. **Wasp species**	Spider genera (% of total orb-weavers)																											
	Eustala	*Araneus*	*Neoscona*	*Argiope*	*Alpaida*	*Parawixia*	*Acanthepeira*	*Pararaneus*	*Micrathena*	*Gasteracantha*	*Larinia*	*Eriophora*	*Dolichognatha*	*Gasteracantha*	*Singa*	*Metepeira*	*Metazygia*	*Mangora*	*Uloborus*	*Plesiometa*	*Tetragnatha*	*Araniella*	*Verrucosa*	*Cyclosa*	*Acacesia*	**n (most abundant genera)**	**% of total orb-weavers**	**% of total**
[25]*T. spinosum*																			69.2							9	69.2	12.7
[33]*T. striatum*	45.1		39.4																							60	84.5	81.0
[16]*T. striatum*	58.5	32.3																								59	90.8	90.8
[22]*T. subimpressum*			21.3																	34.9						153	56.2	40.6
[23]*T. subimpressum*	42.1															42.1										16	84.2	37.2
[14]*T. tenoctitlan*																42.7	53.8									382	96.5	46.7
[31]*T. texense*	41.7																				44.4					31	86.1	44.3
[27]*T. tridentatum*	32.2															29.9										322	62.1	40.9
[13]*T. tridentatum*	85.2			9.1																						351	94.3	68.2
[13]*T. tridentatum*		10.0									90.0															10	100	58.8
[13]*T. tridentatum*		47.4									36.8															16	84.2	23.8
[35]*T. tridentatum*																100										182	100	100
[13]*T. tridentatum*	28.5																					51.5				104	80	29.8
[15]*T. vagulum*	30.2																						17.1	17.1		335	64.4	61.0

Capítulo 3

Variation in the stabilimenta of *Cyclosa fililineata* Hingston 1932 and *Cyclosa morretes* Levi 1999 (Araneae: Araneidae) in Southeastern Brazil



VARIATION IN THE STABILIMENTA OF *CYCLOSA FILILINEATA* HINGSTON, 1932 AND *CYCLOSA MORRETES* LEVI, 1999 (ARANEAE: ARANEIDAE) IN SOUTHEASTERN BRAZIL

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Running title: The stabilimenta of *Cyclosa fililineata* and *C. morretes*

ABSTRACT

In this study we investigated the characteristics of the stabilimenta constructed by two species of *Cyclosa*, describing the variations within and among five populations of Southeastern Brazil. We collected a total of 563 stabilimenta of *Cyclosa fililineata* and 202 of *Cyclosa morretes*. Both species construct stabilimenta composed entirely of silk (linear and spiral types) or by silk and debris (linear; row of detritus clusters and complex types, including detritus positioned in a shape that resemble a large spider). The vertical linear type, containing detritus, was the most frequent structure for adult females of both species. Stabilimenta composed by a row of detritus clusters, however, were more frequent for juveniles of *C. morretes*. These structures seem to be an intermediate state towards the linear continuous type usually found in adults. The other types were rarely found, and silk stabilimenta seems to be constructed only when detritus are not available, as after web destruction. The substitution of silk by detritus suggests that both devices function as camouflage in *C. morretes* and *C. fililineata*. The positions occupied by the spiders within the detritus column (and in some cases the stabilimenta orientation) are highly variable within populations, and the unpredictability of their location may be important to reduce the risks of predation. The protective hypothesis is also corroborated by the observation that the size of spiders is strongly correlated with both width and length of their stabilimenta.

Key-words: Stabilimentum, *Cyclosa*, orb-web, Araneidae.

INTRODUCTION

Stabilimenta are silk or detritus devices included by some spider species in the hub or close to the hub of their webs. These structures had independently appeared at least nine times during the evolution of orb web spiders, always in species whose webs are exposed during the day (Scharff & Coddington 1997, Herberstein *et al.* 2000). Herbestein *et al.* (2000) found reports of web decorations in 22 genera of the families Araneidae, Tetragnathidae and Uloboridae, but new registers are continuously being added to this list (e.g. *Allocyclosa* - Levi 1999, Eberhard 2003; *Molinaranea* - Levi 2001; *Metepeira* - Piel 2001; *Verrucosa* - M.O.Gonzaga, pers. obs.). Some stabilimenta, as those of some species of *Micrathena* and *Gasteracantha* (Araneidae), are composed generally by small silk flocks and, therefore, are considered by some authors as non functional structures (see Nentwig & Heimer 1987). Others, as those of *Argiope* (Araneidae), are very conspicuous and present different shapes and sizes, depending on the age (Nentwig & Hogg 1988), size (Schoener & Spiller 1992), and nutritional condition of the spiders (Blackledge 1998, Herberstein 2000).

Several species of *Argiope* display a high within-species ontogenetic variation in the forms and frequency of decorations. Juveniles of *Argiope savignyi*, for example, usually construct discoid decorations, while the adult females construct cruciate stabilimenta more often (Nentwig & Heimer 1987). Schoener & Spiller (1992) found that *A. argentata* with intermediate sizes build cruciate stabilimenta in a higher frequency than small and large individuals. They argued that the cruciate stabilimenta may have the function of altering the apparent size of spiders. As lizards are major predators in their study areas (islands in Bahamas), and are gape-limited, spiders with a large apparent size may be less susceptible to attacks. Thus, large spiders don't need to appear much larger still, and smallest individuals can not build cruciate structures because acting like that they would appear just like medium sized spiders, which are suitable prey for lizards. The proportion of individuals that decorate their webs can also be very distinct between populations. Hauber (1998), for example, showed that only about 25% of *A. appensa* individuals from Guam build stabilimenta. Kerr (1993), studying other populations of this same species on neighbouring Pacific islands found frequencies of web decorations varying from about 4 to 76%.

In the genus *Cyclosa*, the majority of the known species adds web threads, debris and egg sacs to the central region of the webs, forming linear continuous structures (Levi 1977), linear discontinuous (Rovner 1976), spiral (McClintock & Dodson 1999) or more complex types (M.O. Gonzaga, pers. obs.). According to Nentwig & Heimer (1987) each species present a specific stabilimentum pattern, but few of them were described considering intraspecific variation (see Levi 1977, 1999, Herberstein *et al.* 2000). This variation may be very important in the investigation of the functional explanations of these structures. Craig (1994a, 1994b), for example, showed that the stingless bee *Trigona fuviventris* is capable of learning to avoid webs of *Argiope argentata* decorated with the same pattern of stabilimentum over successive days. When the orientation of these devices was varied, however, bees were more likely to be intercepted in the web threads. These results indicate that an unpredictable decorating behaviour may reduce the probability of association of a specific pattern with the presence of a web by potential prey and/or predators and parasitoids.

The goals of this study are to determine if there are species-specific patterns of stabilimenta in the *Cyclosa* species of Southeastern Brazil and to describe the intraspecific variation of this structure within and between populations of the two most abundant species. We also followed the process of reconstruction of stabilimenta after the removal of the original structure to verify if some previously identified kinds of decorations are just intermediate stages toward the construction of other types.

MATERIAL AND METHODS

The samples were conducted in five areas of Southeastern Brazil (Fig. 3.1), from December 1999 to December 2000, by visual search along forest borders and in forest interior. Each area was sampled three times, with an interval of three months between two surveys. Surveys were scattered in the time to assure the sampling of individuals in different maturation stages.

We registered the width (close to spider position) and total length of the column of detritus, and length of the superior and inferior segments of the stabilimentum, for all webs located. Spiders and their stabilimenta were collected to be measured in laboratory, using a dissecting microscope with a ocular micrometer. In order to keeping stabilimenta dimensions unaltered during transportation, we fixed these structures in cardboards using a thin layer of glue.

These data were used in comparisons of stabilimenta characteristics between species and populations, and to calculate an index of symmetry of the detritus column described by the equation: IS=(((E/2)-A)/E)*2 (where E=total length of the column and A=distance between the spider and the superior extremity of the column). This index varies between -1 and 1. An index with value 0 means that the spider is located exactly in the middle of the column. In addition to the symmetry of stabilimentum, we registered the inclination of these structures using a circular grid positioned behind the spider (see McClintock & Dodson 1999).

We used the Mann-Whitney U-test to compare the adjustment of abdominal width of spiders with the width of the detritus column between *Cyclosa* species. The adjustment was calculated subtracting the larger width of the abdomen by the width of the stabilimentum in the position just above the hub of the web. The relations between abdominal width and the width of the stabilimentum, and spiders body length and the length of their decorations, within species, were investigated by regression analysis considering the pooled data of all populations.

We also removed the stabilimenta of 126 individuals of *Cyclosa fililineata* (70 adult females and 56 juveniles) and 63 individuals of *C. morretes* (15 adult females and 48 juveniles) to following the process of rebuilding. For this, we completely destroyed the original webs, keeping just the bridge thread, from which the spider starts the construction of a new web. The web and stabilimenta parameters mentioned before were measured for the original web and in 24h intervals after stabilimentum removal. These observations were performed for a period varying from 72 (for adults) to 120h (for juveniles).

RESULTS

Cyclosa fililineata and *Cyclosa morretes* built basically the same five types of stabilimenta: linear structures containing silk and debris, incomplete columns characterized by one to many blobs of silk and debris, complex types (often remembering a large spider), spiral shapes composed only by silk, and linear silk structures (Fig. 3.3). Adult females of both species constructed linear detritus columns in a higher frequency than any other type of stabilimentum. However, linear discontinuous stabilimenta were found very often in webs of immature individuals of *Cyclosa morretes*. Complex detritus structures and both kinds of silk stabilimenta were rarely found in all the studied populations (Fig. 3.4 and 3.5).

The adjustment between the abdomen of the spiders and their stabilimenta was different between species (Mann-Whitney, U=6329.0, $n_{C.fililineata}$=287, $n_{C.morretes}$=80, p<0.001). *Cyclosa fililineata* presented a better adjust. The mean difference between spiders and their stabilimenta in this species was 0.21±0.15mm, while in *C. morretes* the mean difference was 0.47±0.37mm. The dimensions of the stabilimenta varies in function of spider size. The width of the column close to spider position was strongly correlated with the abdomen width for both species (r^2=0.49, F=273.6, p<0.001, n=287 for *C. fililineata* and r^2=0.60, F=118.1, p<0.001, n=80 for *C. morretes*) (Fig. 3.6), as well as the length of the column with spider body length (r^2=0.48, F=368.5, p<0.001 for *C. fililineata* and; r^2=0.42, F=68.9, p<0.001 for *C. morretes*) (Fig. 3.7). Most stabilimenta in all populations were constructed in a vertical position, but this orientation is not obligatory for these species (Fig. 3.8).

The symmetry of the stabilimentum varies in all the populations studied, especially in webs *C. fililineata*. In spite of that, the frequency of occupation of the extremities of the columns was always lower than the occupation of the central positions in this species (Fig. 3.9). *Cyclosa morretes* was generally found occupying the inferior extremity of the column in P.N. Itatiaia and in P.E. Intervales. In Floresta da Cicuta, however, we found several individuals in the inferior extremity but also a large proportion in central positions (Fig. 3.10).

The pattern of the original stabilimentum, in most cases a linear structure with detritus, was reconstructed in the great majority of the webs of females and juveniles of *C. fililineata* after a 72h interval (Figs 3.11 and 3.12). Several webs constructed in the day after the removal of the original stabilimentum contained the otherwise rare linear and spiral silk structures. The occurrence of silk stabilimenta in the first day after web destruction was also observed in females and juveniles of *C. morretes*. In immature individuals of this species, however, the frequency of linear detritus structures after 120h still was relatively low. In adults, we observed that linear silk stabilimenta are gradually substituted by detritus as soon as spiders have access to prey items or collect debris intercepted by the web (Fig. 3.13 and 3.14). In spite of that, stabilimenta composed totally or partially by silk persisted for a long time in *C. morretes* juveniles (Fig. 3.15).

DISCUSSION

All kinds of stabilimenta, except the complex shape with detritus, observed in webs of *Cyclosa fililineata* and *C. morretes*, were previously described for other species of this genus (see Levi 1999, McClintock & Dodson 1999, Rovner 1976, Tso 1998). Our comparisons among populations showed that the proportions of these types are similar for each species in different localities. Linear detritus structures are the commonest type constructed by *C. fililineata* and also by females of *C. morretes*. Unlikely the discontinuous columns (blobs of detritus), this shape completely disrupt the visual sign of a spider. This could be an indicative that the function of these stabilimenta is associated with protection, possibly reducing the probability of spider localization by visually oriented predators. The disruptive function is also supported by our results regarding the adjustment of stabilimentum width with the width of spider's abdomens. The width of the column follows the size of spiders, otherwise their positions would be revealed.

The placement of blobs of detritus, however, may also be a good strategy to avoid predators, specially in situations when spiders have to deal with a very limited amount of detritus. The blobs frequently present about the same size of a spider and predators may be confused during the attacks. If they attack a wrong target (a blob located far from the spider body), the spider may have time enough to escape running or jumping from the web. The complex type seems to be a derivation of a blob, larger and frequently containing some projections resembling legs.

Herberstein *et al.* (2000) argued that extrapolations from one phylogenetic group to another are unlikely to be relevant in resolving the debate about functions of web decorations, and that structures containing debris probably should not be considered as 'decorations' or 'stabilimenta', but as a separate behavioural phenomena. Our results, however, showed that the linear structures containing detritus constructed by at least two *Cyclosa* species are initially composed just by silk, being very similar to the linear stabilimenta of many uloborids. Eberhard (2003) described the same pattern of substitution of one type for another in *Allocyclosa bifurca* and in *Cyclosa monteverde*. In addition, he showed that these species are refrained from constructing silk stabilimenta when egg sacs are available. These data suggest that the possible function of silk decorations can be accomplished by a structure containing egg sacs or detritus, and that these different devices are just variations of a same behavioural unit.

The observation that detritus are placed over silk stabilimenta (but never the opposite) argue against the hypothesis that these last devices are used for prey attraction. Detritus probably would interfere with any reflective property of the silk stabilimenta, reducing their effectiveness in attracting insects searching for UV signals. Alternatively, silk linear and spiral stabilimenta may also disrupt the shape of a spider, although being less effective and, because of it, replaced as soon as possible.

Neet (1990) proposed another explanation for the spiral stabilimenta constructed by *Cyclosa insulana.* He argued that this kind of stabilimentum may have the function of conferring mechanical stability for the orb-webs under strong wind conditions. His conclusion, however, is based just on the observation that spiral stabilimenta are constructed in a higher frequency after stormy nights with strong winds. These results may be just a consequence of a higher incidence of web destruction under these weather conditions. Losing their original linear stabilimenta, spiders can not build another similar device simply because they don't have detritus available to be incorporated on the webs. The hypothesis of mechanical stability must be tested submitting webs with spiral and linear silk stabilimenta to controlled wind intensities and measuring their resistance.

The variation in stabilimentum symmetry within many of the studied populations could represent a factor of unpredictability that may also be important to avoid predators. There is no evidence that spider predators are able of associating the shape of stabilimenta with the presence of their prey (see Blackledge & Wenzel 2001). In spite of that, if this eventually happens, they will have to locate the spider in the middle of the detritus column. Attacking always a specific position, predators will fail most of the times. It's not clear, however, why *C. morretes* occurs more frequently in the inferior extremity of their detritus column. This position may promote a faster response after the detection of a vibrational stimuli in the web, but we have no data to support or refuse this hypothesis.

A final component of variability detected in this study was the orientation of the stabilimenta. Although most structures presented a vertical position, we found stabilimenta deviating from this direction in all the studied populations. According to McClintock & Dodson (1999) this variation in *C. insulana* may be related with the predominant orientation of elements of the background, reducing the visibility of decorations. Rovner (1976), however, showed that the orientation of the stabilimenta constructed by *C.*

turbinata is determined exclusively by geotaxis. The significance and reasons of variation in stabilimenta directions also remain to be appropriated tested.

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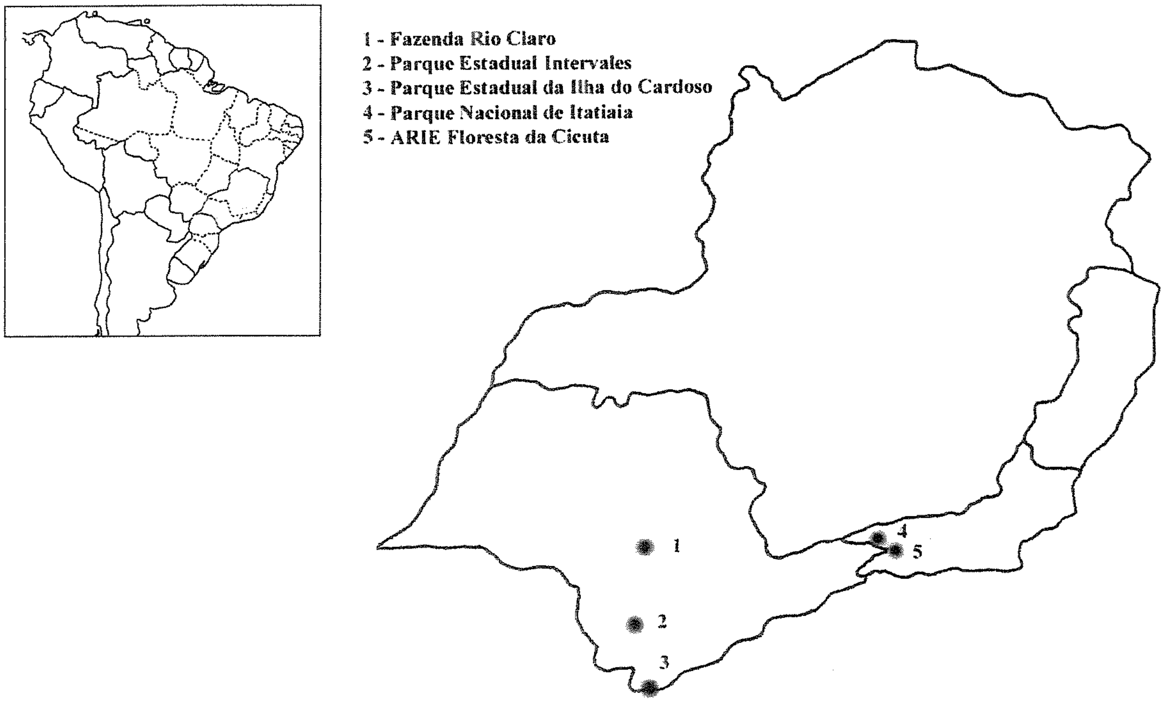


Fig. 3.1: Study areas in Southeastern Brazil. 1, 2 and 3 in São Paulo state; 4 and 5 in Rio de Janeiro state.

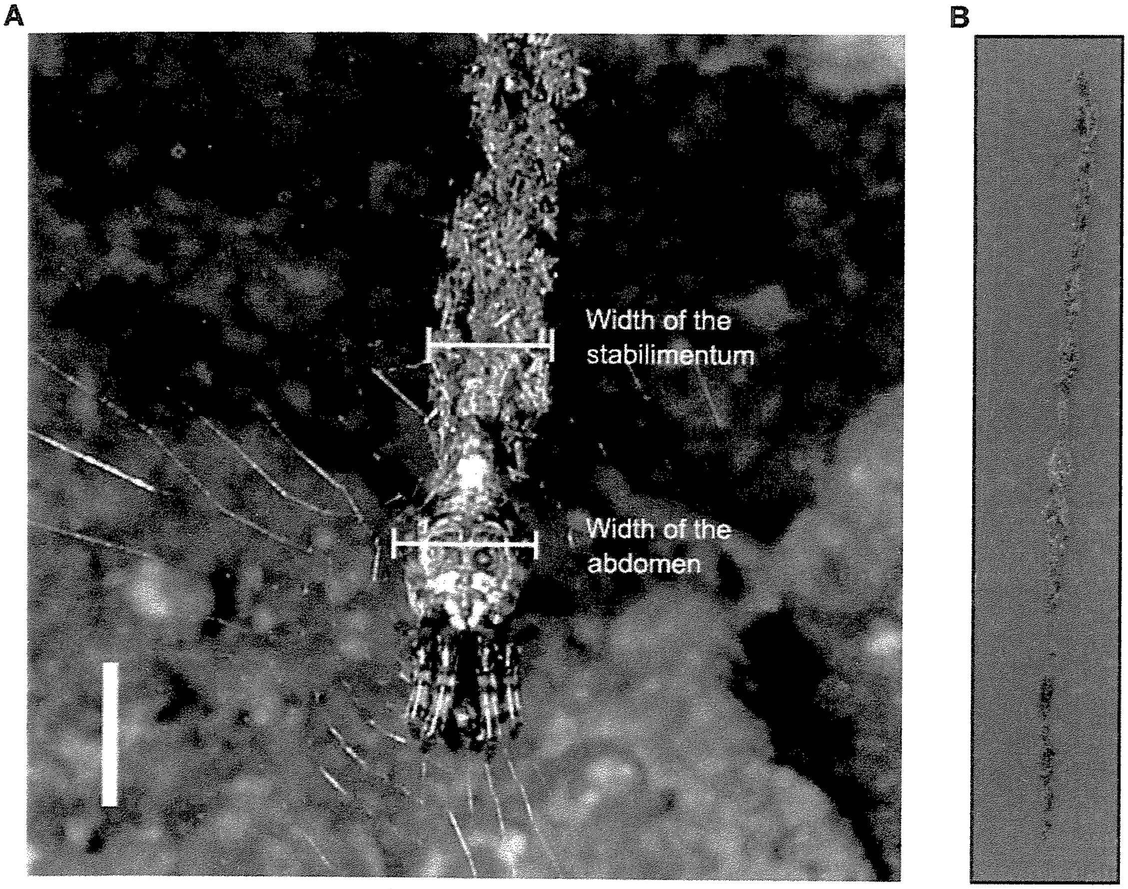


Fig 3.2: (A) *Cyclosa morretes* resting at the hub of its web. We measured the width of abdomen at its widest portion and the width of the stabilimentum in an adjacent position. (B) Cardboard with a stabilimentum of *C. morretes*. Scale: 0.5mm.

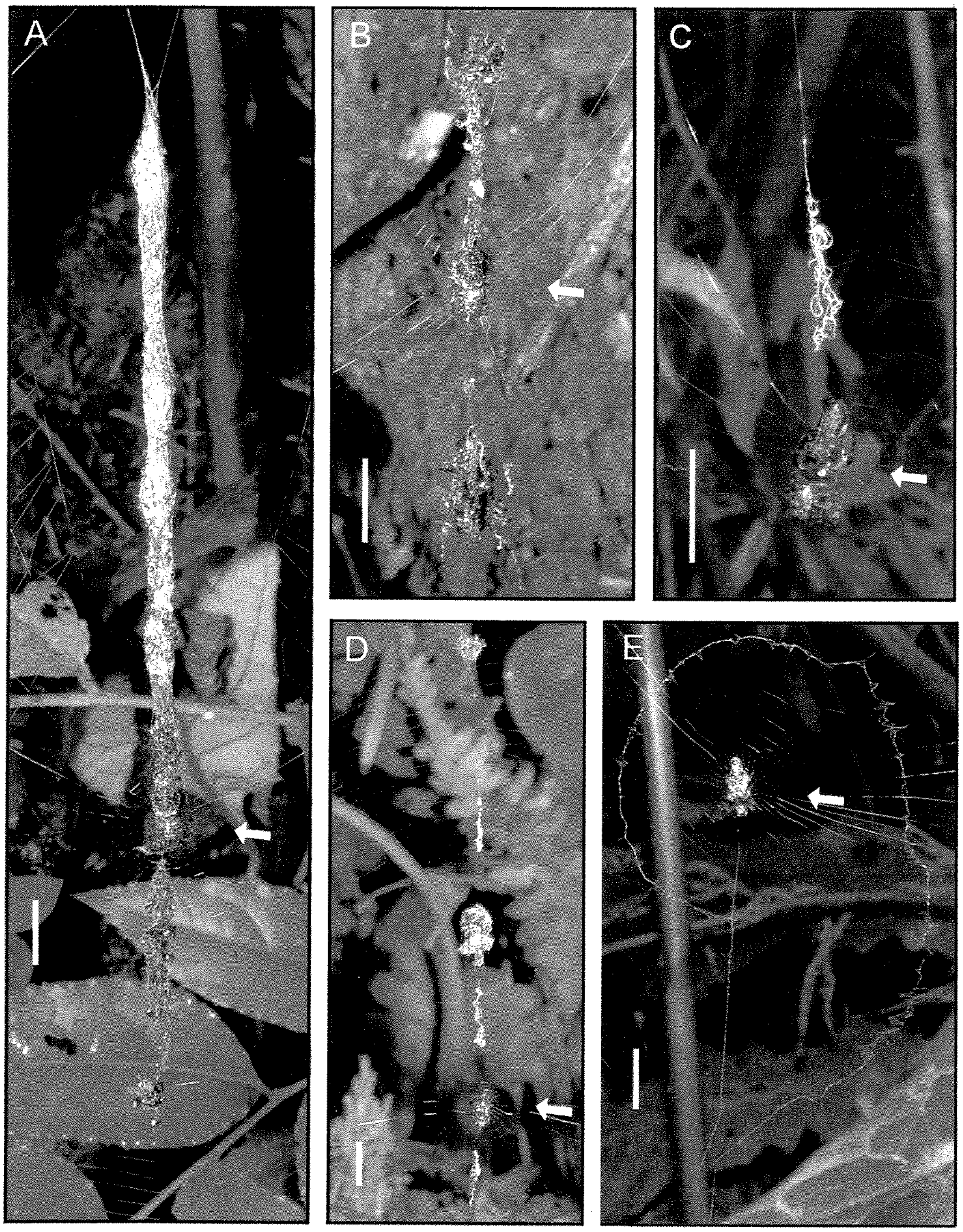


Fig. 3.3: Decoration patterns observed in *C. morretes* and *C. fililineata* webs. (A) Linear detritus structure, (B) complex type, (C) linear silk structure, (D) blobs of detritus composing a linear discontinuous structure, (E) silk spiral. The arrows indicate the position occupied by the spider. Scales: 1cm.

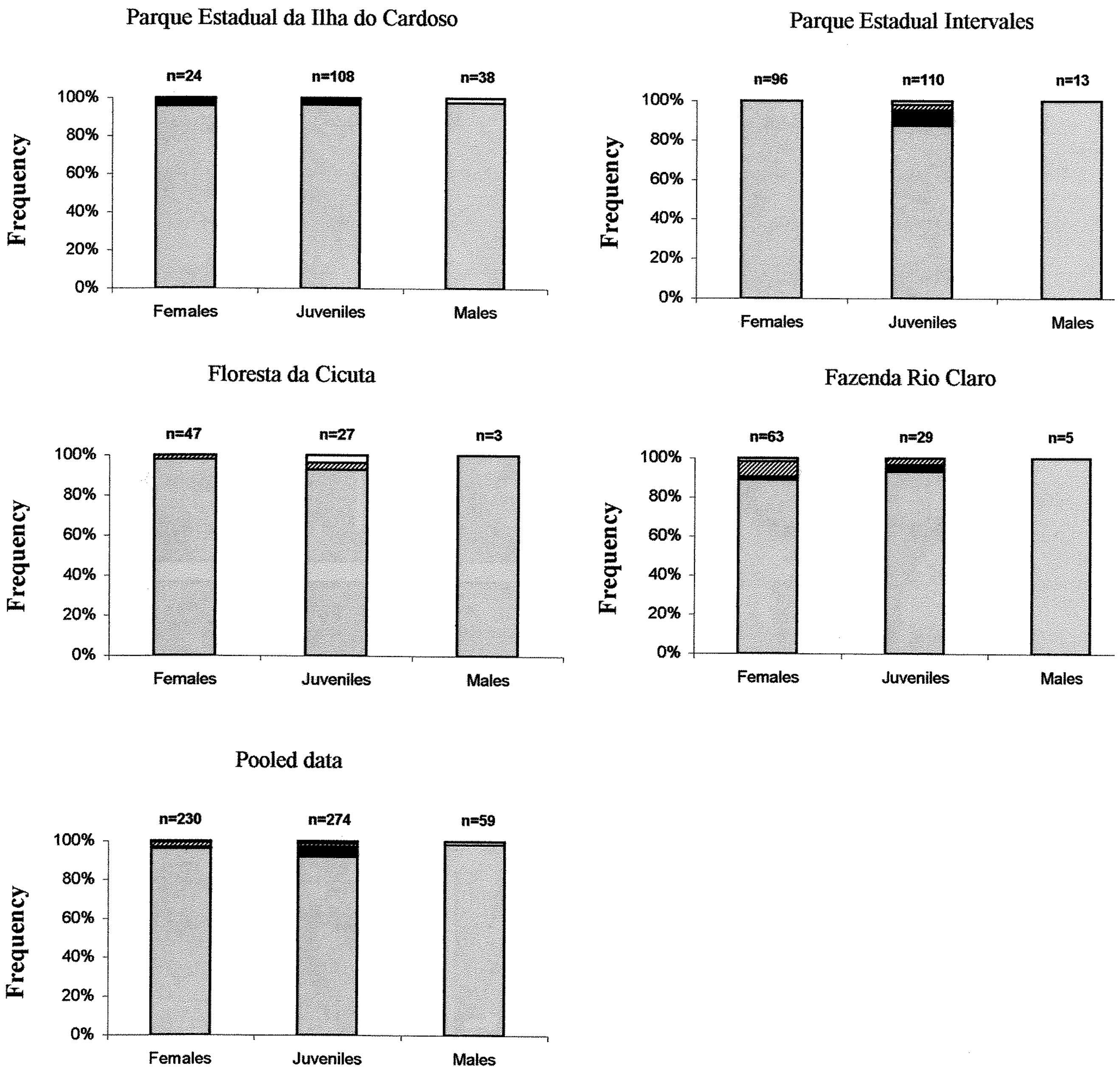


Fig. 3.4: Frequencies of web decorations constructed by *Cyclosa fililineata* in four study areas. Grey bars = linear structures with detritus; black bars = linear discontinuous structures with detritus (blobs bars with diagonal lines = complex types with detritus; white bars = linear silk + spiral silk stabiliment

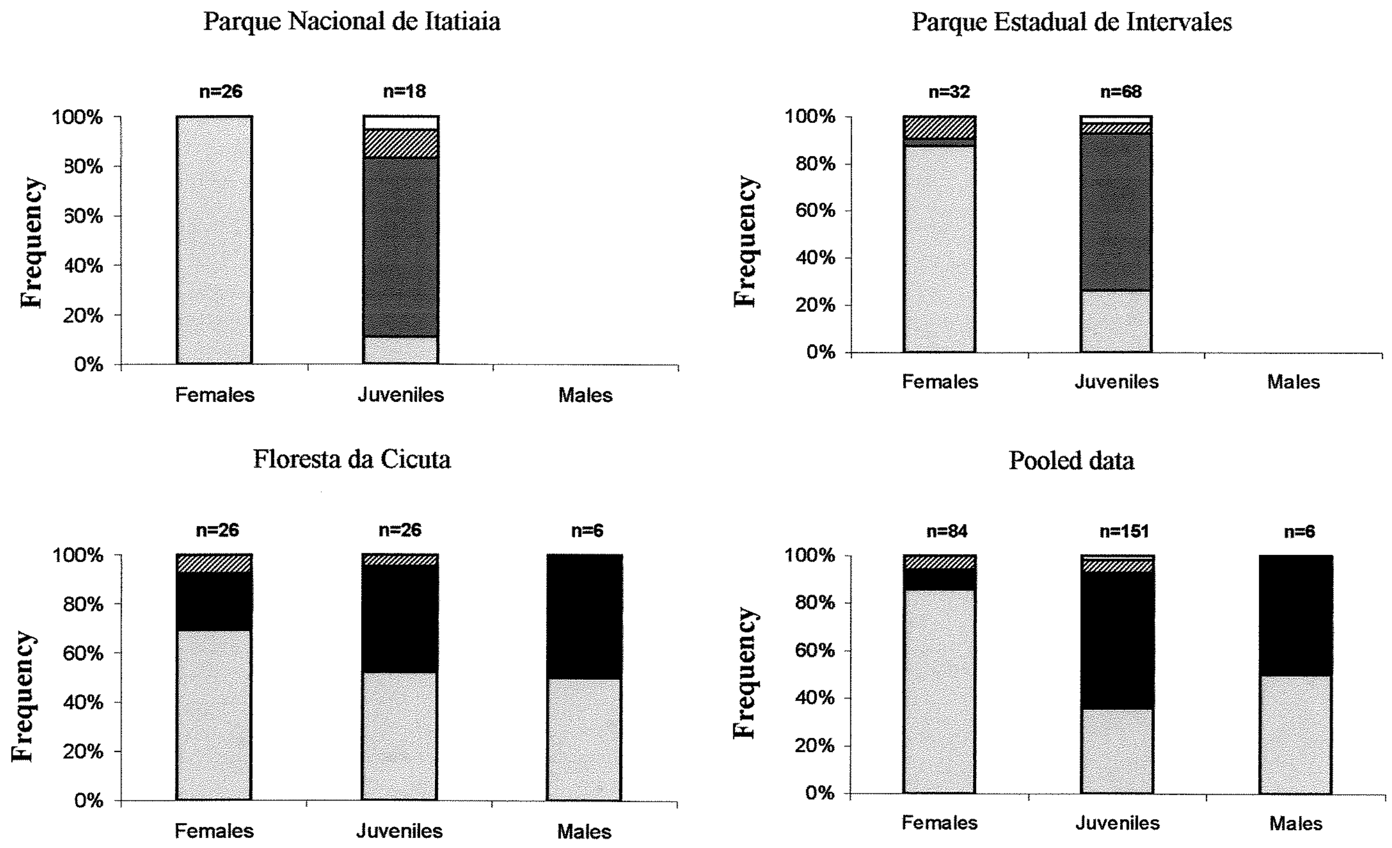


Fig. 3.5: Frequencies of web decorations constructed by *Cyclosa morretes* in three study areas. Grey bars = linear structures with detritus; black bars = linear discontinuous structures with detritus (blobs); bars with diagonal lines = complex types with detritus; white bars = linear silk + spiral silk stabilimenta.

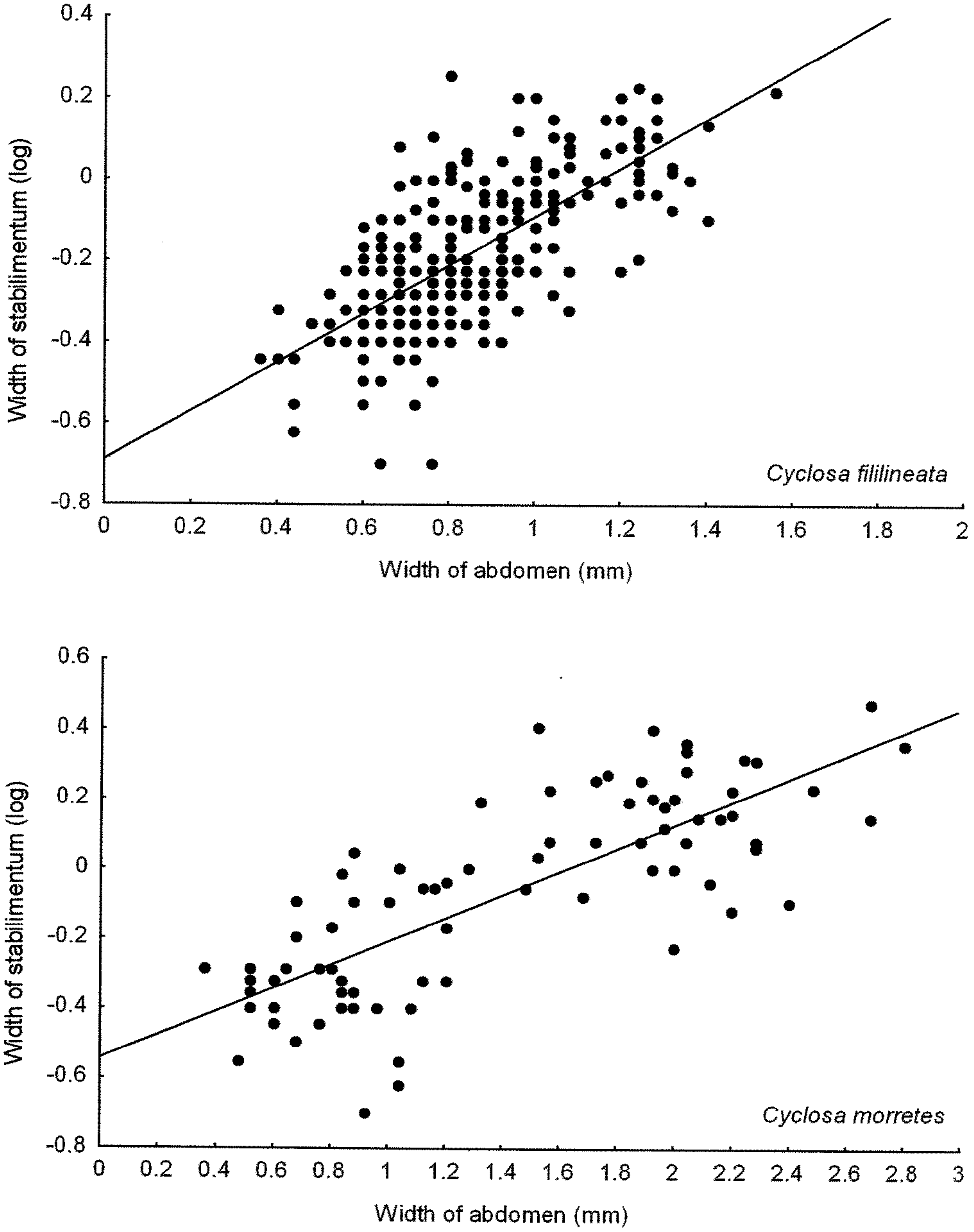


Fig. 3.6: Relation between abdominal width and the width of the linear detritus stabilimenta constructed by *Cyclosa fililineata* and *Cyclosa morretes*. Pooled results for adults and juveniles from all populations.

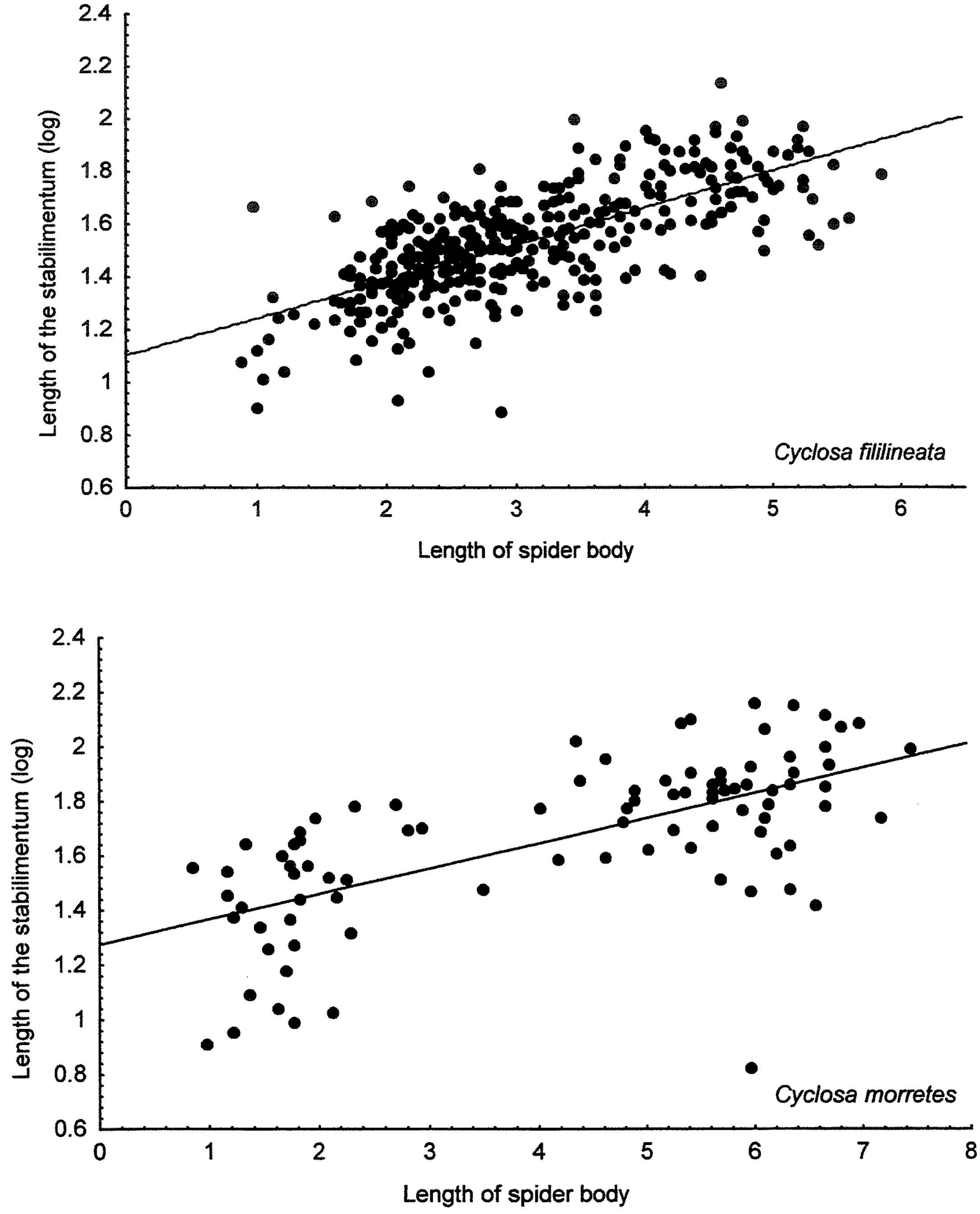
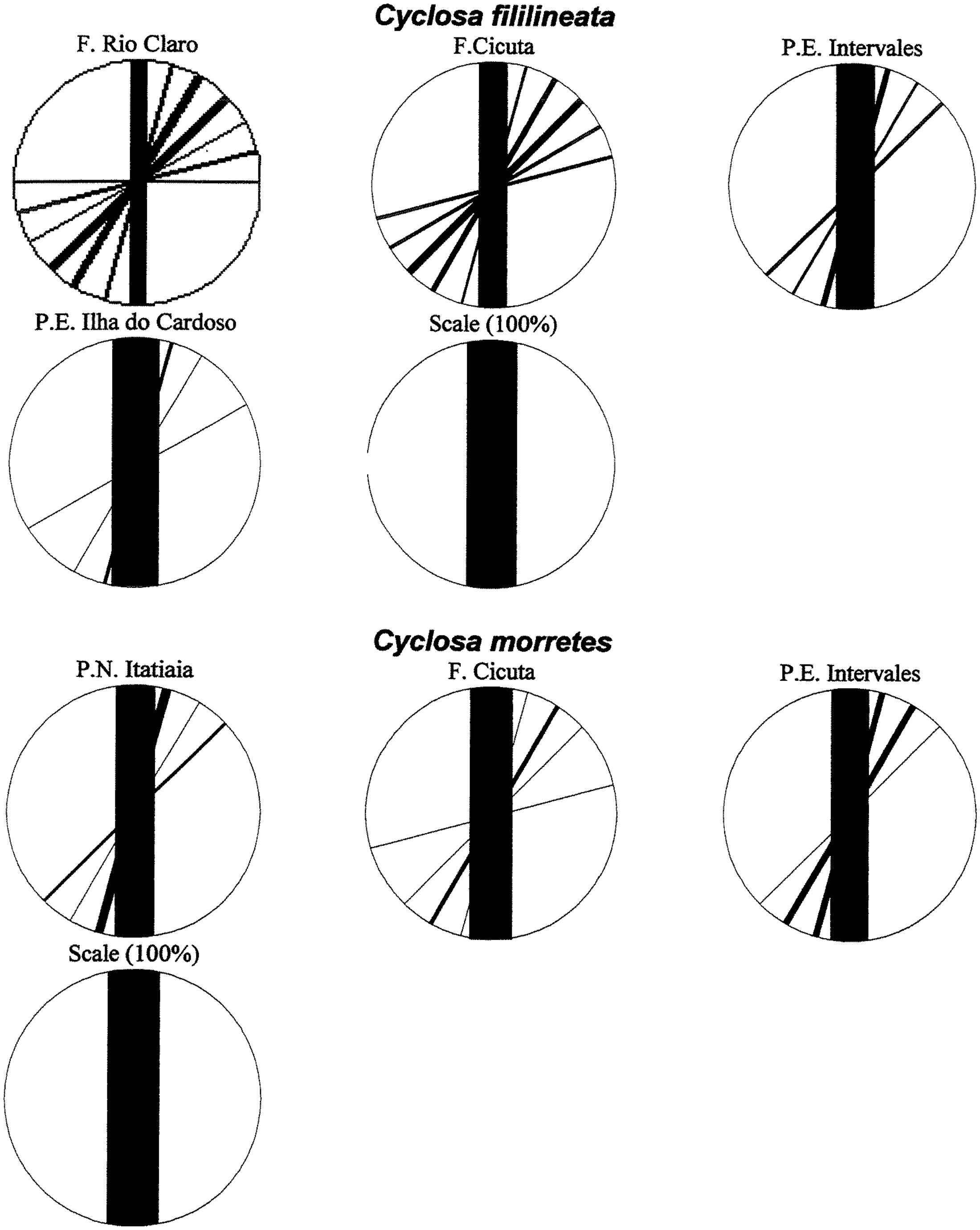


Fig. 3.7: Relation between the length of spider body and the length of the linear detritus stabilimenta constructed by *Cyclosa fililineata* and *Cyclosa morretes*. Pooled results for adults and juveniles from all populations.


Cyclosa fililineata

F. Rio Claro

F.Cicuta

P.E. Intervales

P.E. Ilha do Cardoso

Scale (100%)

Cyclosa morretes

P.N. Itatiaia

F. Cicuta

P.E. Intervales

Scale (100%)

Fig. 3.8: Frequencies of each class (15° intervals) of inclination of the stabilimenta constructed by *C. fililineata* e *C. morretes*. The thickness of each bar indicates the percentage of each category found in the field. Pooled results for juveniles and adults.

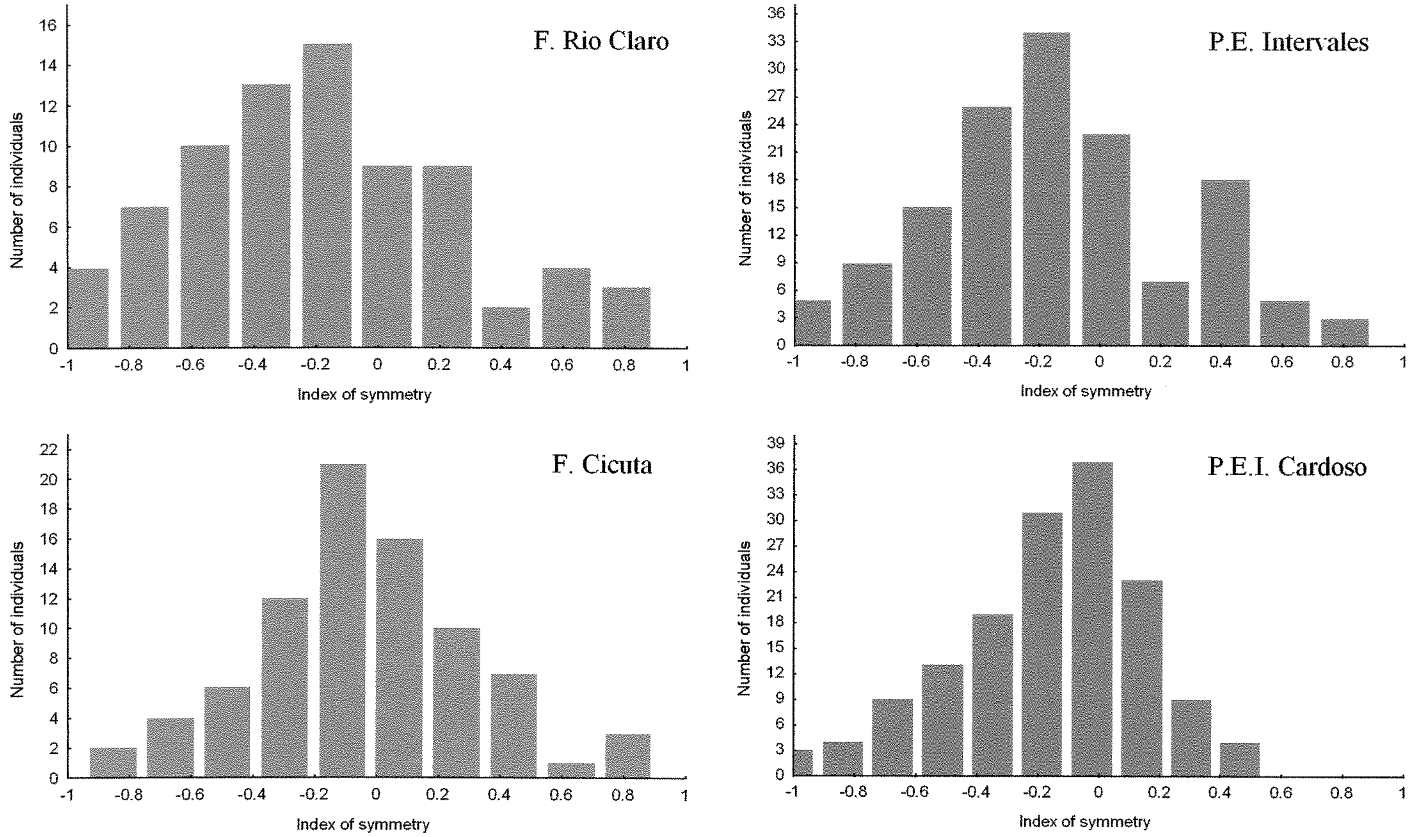


Fig. 3.9: Positions occupied by *C. fililineata* adult in the detritus column in each population. –1=inferior extremity, 0=center, +1=superior extremity.

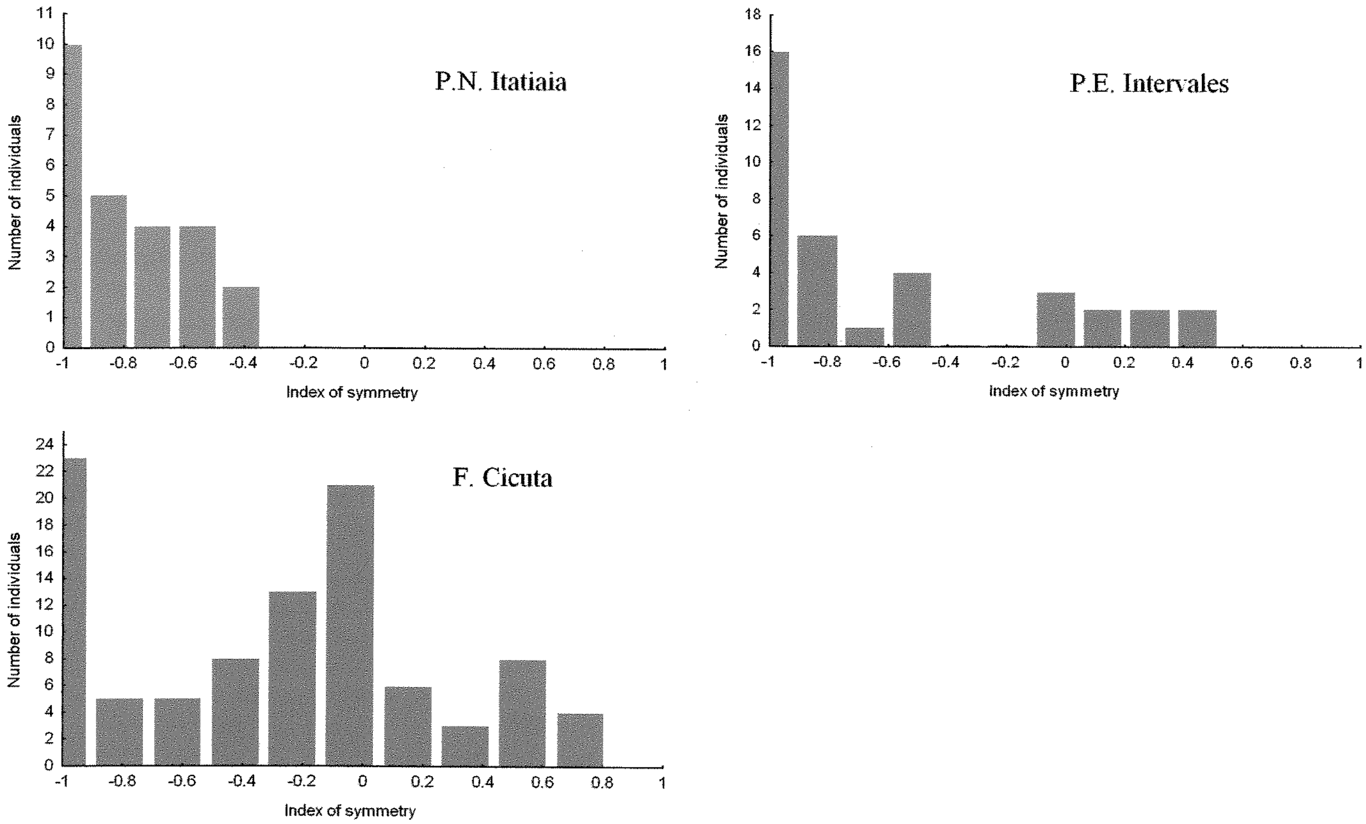


Fig. 3.10: Positions occupied by *C. morretes* in the detritus column in each population. –1=inferio extremity, 0=center, +1=superior extremity.

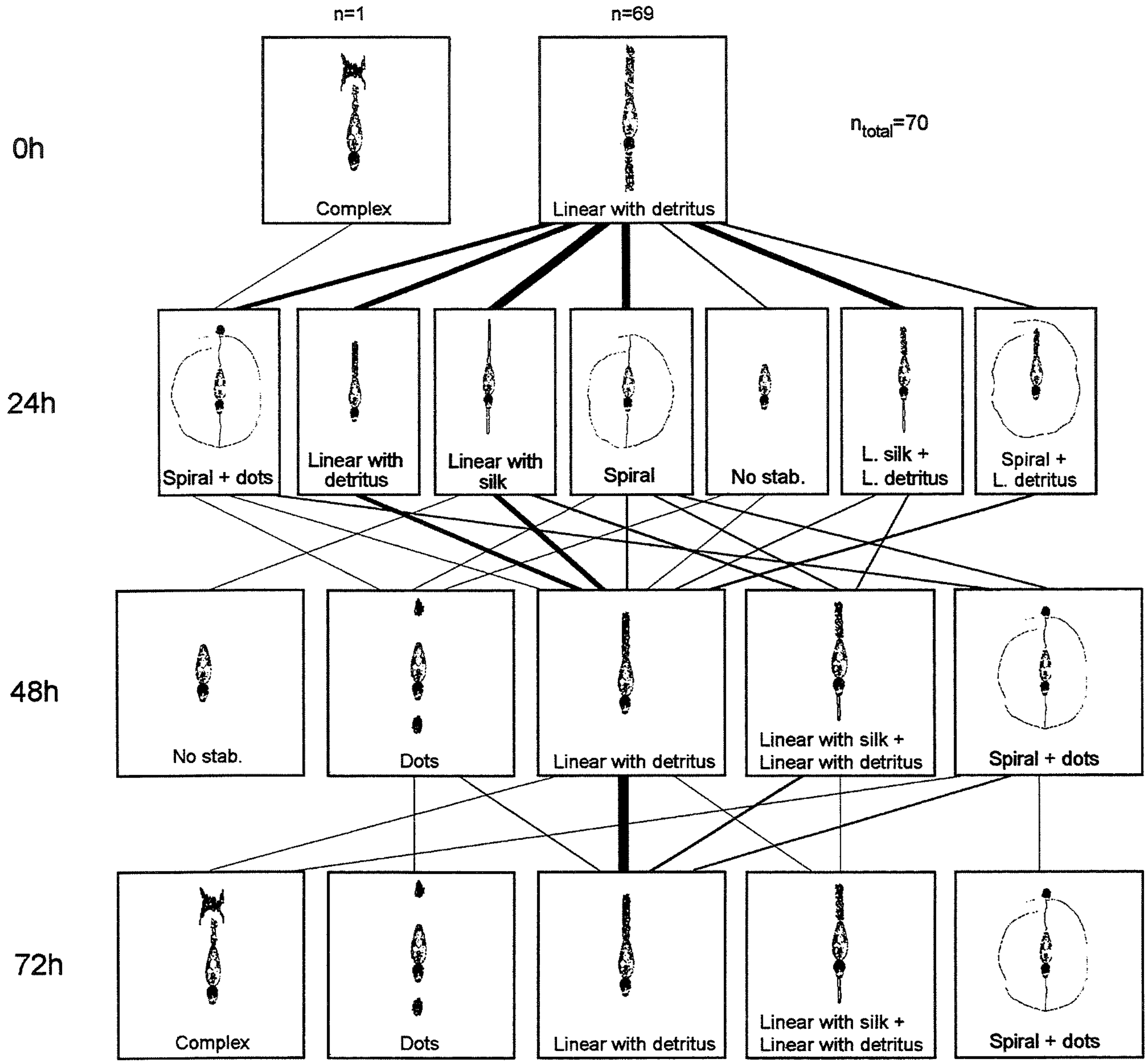


Fig. 3.11: Process of stabilimenta reconstruction of *Cyclosa fililineata* adult females. The thickness of the lines indicates the number of webs that passed to the next stage.

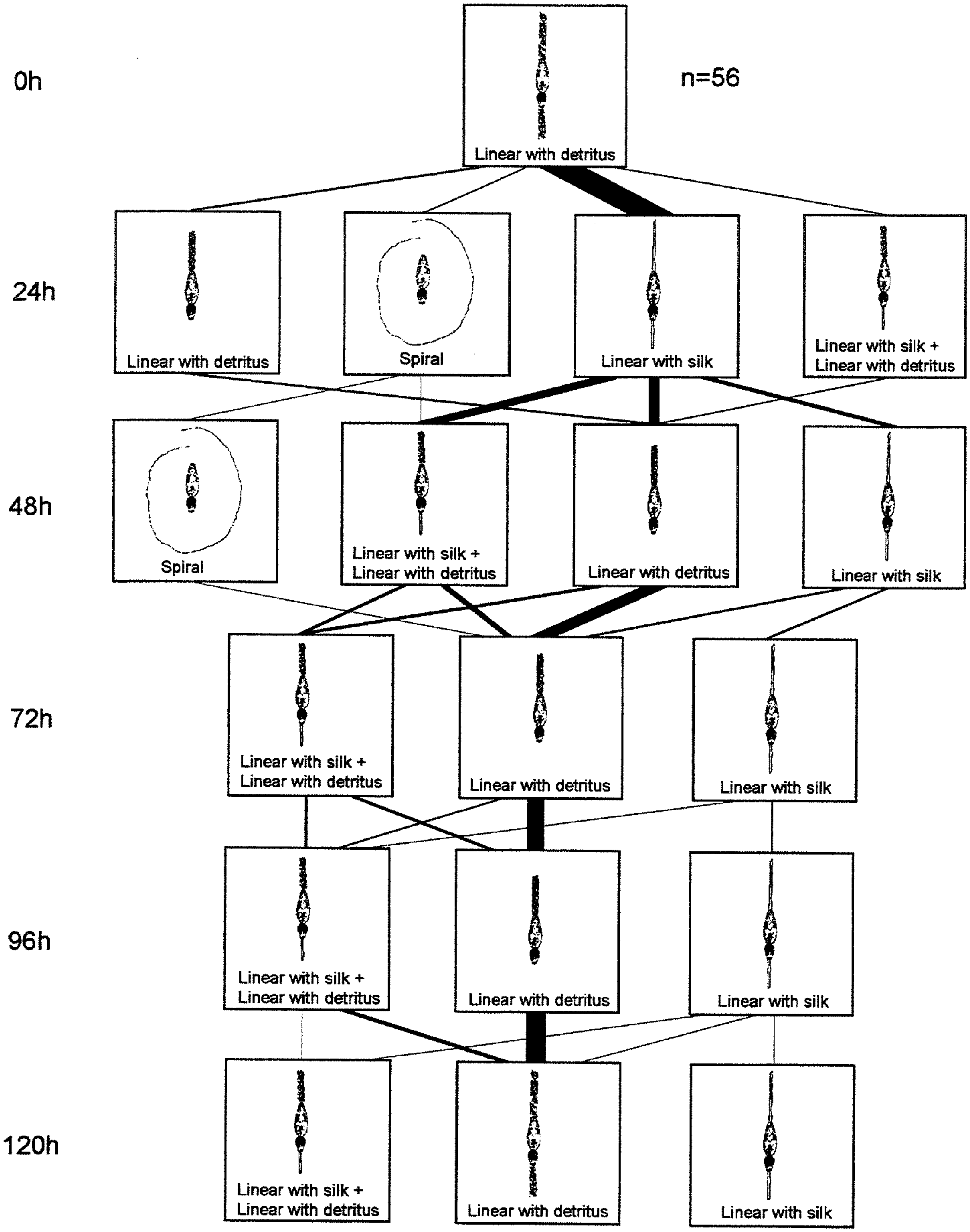


Fig. 3.12: Process of stabilimenta reconstruction of *Cyclosa fililineata* juveniles. The thickness of the lines indicates the number of webs that passed to the next stage.

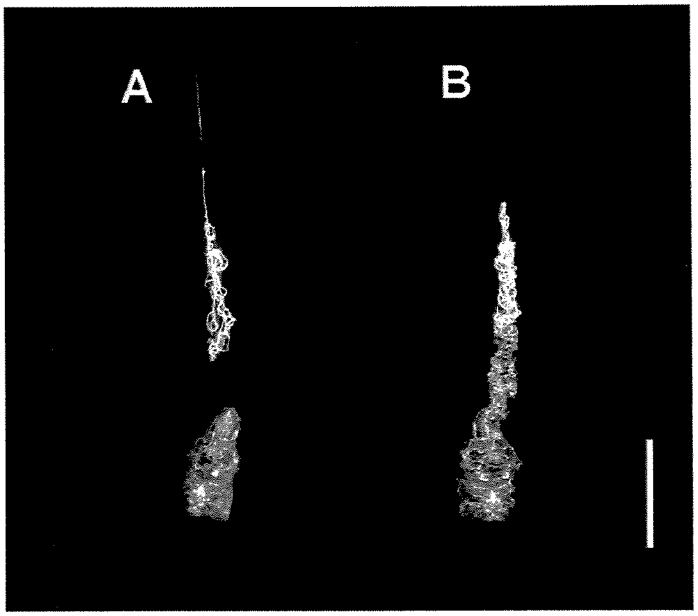


Fig. 3.13: Stabilimentum reconstruction by a *Cyclosa morretes* female. A – Silk stabilimentum present in the web 24h after the destruction of the original structure (detritus column); B – 48h after the destruction the silk stabilimentum is being replaced by a detritus column. Scale: 1cm.

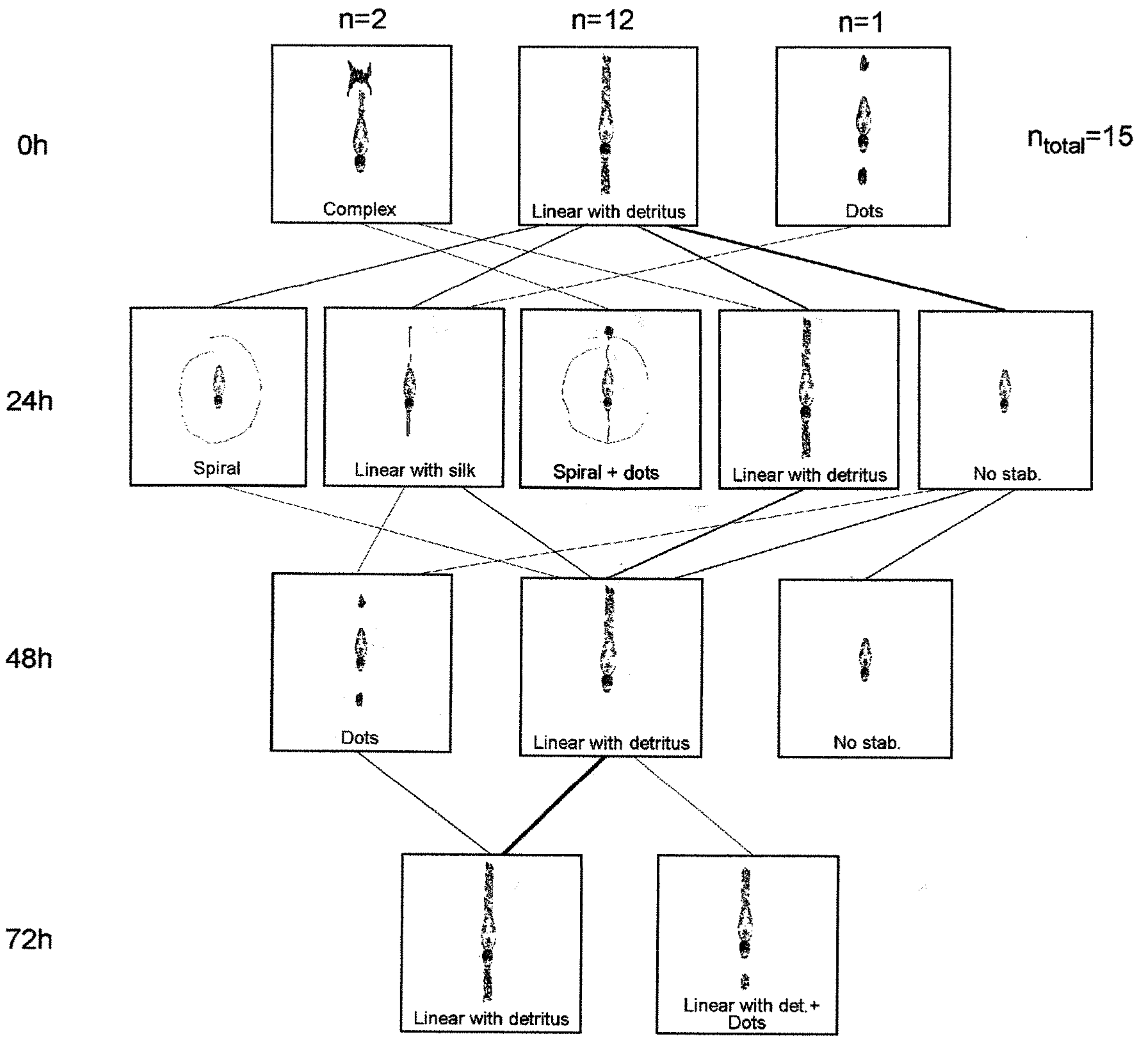


Fig. 3.14: Process of stabilimenta reconstruction of *Cyclosa morretes* adult females. The thickness of the lines indicates the number of webs that passed to the next stage.

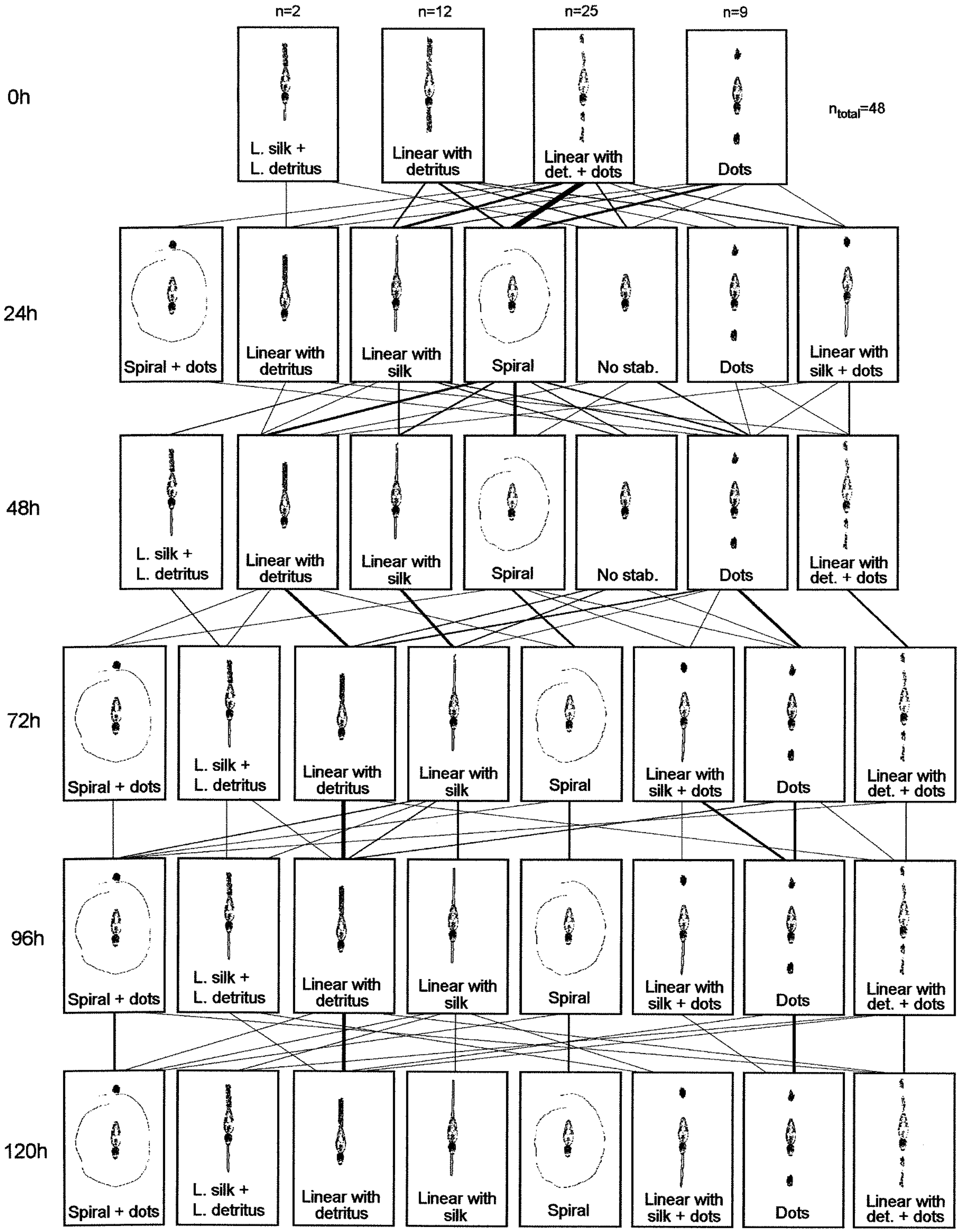
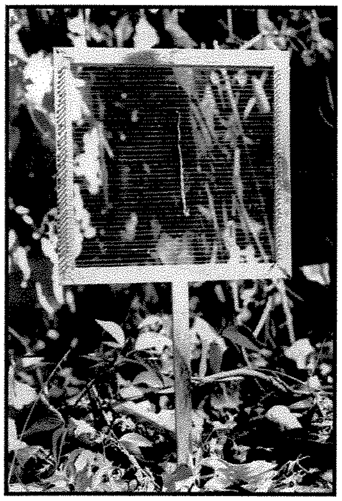
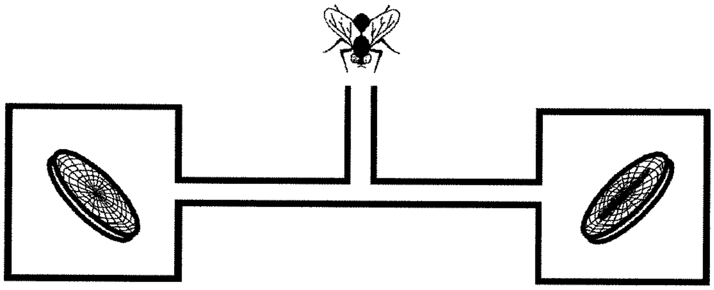


Fig. 3.15: Process of stabilimenta reconstruction of *Cyclosa morretes* juveniles. The thickness of the lines indicates the number of webs that passed to the next stage.



Capítulo 4

Testing the functions of the detritus stabilimenta on the webs of *Cyclosa fililineata* Hingston 1932 and *Cyclosa morretes* Levi 1999 (Araneae: Araneidae): do they attract prey or reduce the risks of predation?



TESTING POSSIBLE FUNCTIONS OF THE DETRITUS STABILIMENTA ON THE WEBS OF *Cyclosa fililineata* HINGSTON 1932 AND *Cyclosa morretes* LEVI 1999 (ARANEAE: ARANEIDAE): DO THEY ATTRACT PREY OR REDUCE THE RISKS OF PREDATION?

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Running title: Functions of detritus stabilimenta

ABSTRACT

Spiders of the genus *Cyclosa* often add prey remains and other debris on their orb-webs. The function of silk decorations generally is associated to defense against predators or to prey attraction, but few studies focused on stabilimenta containing detritus. In this study we used artificial webs with and without the detritus stabilimenta of two species of *Cyclosa* to investigate if these structures increase the number of insects intercepted, and artificial models of spiders and stabilimenta to compare the frequency of attacks against these different shapes. We also conducted a choice experiment in laboratory to test if detritus columns attract *Drosophila melanogaster* to the webs. The interception frequency in webs with stabilimentum was similar to that of webs without such structure. The taxonomic composition and biomass of insects were also similar in both treatments. The choice experiment did not show a significant tendency of attraction to the direction of the recipients containing webs with stabilimentum. On the other hand, models with the shape of a spider were attacked in a higher frequency than those simulating detritus columns and silk decorations. These data argue against the prey attraction hypothesis and suggest that the addition of stabilimenta in webs of *Cyclosa* could reduce predation intensity, possibly by disrupting the visual sign of the spider's outline.

Key-words: Stabilimentum, *Cyclosa*, prey-attraction, predation risk

INTRODUCTION

Among all the proposed explanations to the functions of web decorations, the prey attraction hypothesis has been the most intensively tested and discussed (e.g. Blackledge 1998a, b; Blackledge & Wenzel 1999, Craig & Bernard 1990, Craig *et al.* 2001, Herberstein 2000; Herberstein *et al.* 2000a, b; Tso 1996, 1998a, b). In spite of that, the great majority of data supporting or refusing this hypothesis (and also any other) is restricted to one genus, *Argiope* (Araneidae), while web decorations are widespread among more than 24 genera of orb-web spiders and probably evolved independently at least nine times (Herberstein *et al.* 2000a, Scharff & Coddington 1997, Eberhard 2003).

Craig & Bernard (1990) showed that the zig-zag bands of white silk spun by *Argiope* reflect ultraviolet light. They suggested that this reflection pattern could induce the approximation of pollinating insects searching for UV-bright floral displays. In addition, they discussed the possibility that insects may associate UV-bright patches with open areas free for maneuvering, guiding their flight to the direction of these signs. Some recent studies have provided support to these ideas, comparing prey interception rates of webs with and without stabilimentum (Bruce *et al.* 2001, Herberstein 2000, Tso 1996, 1998a, b) and demonstrating prey attraction in laboratory conditions (Bruce *et al.* 2001, Craig & Bernard 1990, Watanabe 1999). These results, however, contrast with those of Blackledge (1998a, b) and Blackledge & Wenzel (1999, 2000). They argued that objects with a high reflectance of white light+UV are not attractive to insects, having a poor color contrast with the background when considering the insect perception.

The stabilimenta constructed by many *Cyclosa* (Araneidae) species often include a particularity that could make them very different from those of *Argiope*, the addition of prey remains and other debris. In spite of the addition of silk threads to keep the pellets of debris united, the presence of detritus in the decorations probably would affect any reflection property that might attract insects (see Zschokke 2002 for a comparison between UV-brightness of silk and detritus stabilimenta) and some authors suggest that these structures should not be considered as 'decorations' or 'stabilimenta', but as a distinct behavioral phenomena (Herberstein *et al.* 2000).

The construction of a linear detritus stabilimentum in some species of *Cyclosa* and in *Allocyclosa*, however, generally is preceded by silk decorations (Gonzaga & Vasconcellos-Neto in prep., Eberhard 2003, Rovner 1976). Tso (1998b) found that webs with linear silk structures of *C. conica* intercept about 150% more preys than webs without stabilimentum. But, if silk decorations really improve the frequency of prey capture, why this pattern is substituted by a column of detritus as soon as debris are available? Could this second type of stabilimentum keep the property of prey attraction? Blackledge & Wenzel (1999) argue against the prey attraction hypothesis in the case described by Tso (1998b) suggesting that correlation between prey interception and the presence of stabilimenta does not necessarily means that decorations are attracting insects. According to them, a high prey capture may increase the frequency of stabilimentum construction, possibly inducing the same results.

Another interesting aspect involved in the addition of detritus columns in webs of *Cyclosa* is that spiders rest during the day at a position that make their outlines merge with those of their stabilimenta. Eberhard (1973) observed a similar resting position in *Uloborus diversus*, which construct one or more segments of white silk laid in lines along the radii and sometimes a circular kind of decoration also composed by silk. He argue that spider's position, contiguous to these structures, obscure their outline and difficult the recognition of these potential prey for generalist predators searching for spider-like forms.

Despite all the polemic about this issue, few species and kinds of stabilimenta were studied in the genus *Cyclosa*. In this study we test if detritus stabilimenta improves the interception frequency of insects in webs of *C. morretes and C. fililineata* and if the shape of a column of detritus constitute a sign equally attractive to predators as the visual sign of a spider resting in the hub of a web.

MATERIAL AND METHODS

EXPERIMENT 1: ARTIFICIAL WEBS IN THE FIELD

This experiment was conducted in "Área de Relevante Interesse Ecológico Floresta da Cicuta" a small (131 ha) Atlantic Forest fragment located in Volta Redonda (22°31'S 44°07'W), state of Rio de Janeiro, Brazil.

To test if the presence of a column of debris improve the rate of prey interception we constructed 20 artificial webs. The artificial webs were composed by a squared wood frame (15x15cm), containing a net of nylon threads placed parallel one from another (with 3mm of distance) in horizontal position (Fig.4.1). Each frame was attached to a pole to fixation on the ground. We fixed a linear stabilimentum of *Cyclosa morretes* in 10 of these webs and 10 others remained without the column of detritus. The net in each artificial web was covered with an adhesive substance (Tanglefoot® Insect Trap Coating, Tanglefoot Co., Grand Rapids, MI, USA). We selected 10 localities in a map of Floresta da Cicuta, by random sample, to place the webs. In each of these localities we placed one web containing a stabilimentum and another one without this structure at 1 m from each other.

The webs were inspected daily during 5 days. In each inspection all the potential prey items were removed and preserved in alcohol 70% for posterior identification and measurement to determine the total biomass intercepted. The biomass was calculated using the total body length, according to the general equation proposed by Hódar (1996). The comparison between number of preys and biomass in the two treatments was carried out using a paired-sample t-test. When necessary data were transformed to $\log_{10}$ to satisfy the requirements of the parametric test. The same procedure was applied using stabilimenta of *Cyclosa fililineata*, one month later.

EXPERIMENT 2: PREY ATTRACTION IN LABORATORY

We conducted an experiment similar to that described by Craig & Bernard (1990), Watanabe (1998) and Bruce *et al.* (2001) to verify if the detritus stabilimenta could represent a visual sign that attract preys. Two acrylic boxes (20x20x20cm) were constructed with a lateral opening, for the connection of a T-shaped tube (2.0 cm diameter), and a superior opening for illumination. We used a white light source (25W) placed right above this superior opening. The boxes were covered with black paper to control the incidence of light from other directions. In one of these boxes we placed a plastic ring containing an orb-web without stabilimentum and, in the other, a ring containing an orb-web with a linear stabilimentum containing detritus. The rings were placed in a position that aligns the web hub with the center of the tube's exit (Fig. 4.2).

We introduced one individual of *Drosophila melanogaster* (Diptera, Drosophilidae), for each trial, in the opening of the connecting tube and registered the frequency of choice of each box. The rings were switched and the tube was cleaned with water after each trial to avoid site effects and the permanence of chemical cues. The same stabilimentum was presented to at least 30 flies (and no more than 100) and three stabilimenta of each species were used in the tests.

The distance between the rings and the middle of the T-shaped tube was established based on the observation, related by Rypstra (1982), that *D. melanogaster* is able of changing their flight path as approached at a distance of about 2 cm from strands of silk. This avoidance behavior was especially frequent in higher thread densities. Craig (1986) also investigated the minimum distance at which high- and low-fiber-density webs were avoided by *D. melanogaster*. Webs composed by dense fibers were avoided at a distance of 7cm and webs built with thin fibers at 2 cm. Considering these data, we assumed that the visual sign of a stabilimentum placed at about 4 cm (including the length of the tube plus a distance of about 1 cm from the wall of the box) is perceptible by these flies.

EXPERIMENT 3: FREQUENCY OF ATTACKS BY PREDATORS IN THE FIELD

These experiments were performed in the "Parque Estadual Intervales", an Atlantic forest reserve located in Ribeirão Grande (24°16'S; 48°25'W), state of São Paulo, Brazil. This state park comprises an area of 49,000 ha and it's connected to three other conservation units, encompassing a total of 120,000 ha of old second growth and primary evergreen cloud forest.

We used models of stabilimenta and spiders made of odorless, non-toxic modeling clay (Acrilex®, Acrilex Tintas Especiais S.A., SP, Brazil) to test the possible protective function of the detritus column. This same material was previously used to evaluate the effect of color and shape of cactus fruits on detection by lizards (Vasconcellos-Neto *et al.* 2000) and bird preferences for different fruit colors (Alves-Costa & Lopes 2001). Artificial models composed by a similar modeling compound were also used to test the influence of different color patterns of snakes in the frequency of attacks by birds and mammals (Brodie III 1993, Brodie III & Janzen 1995, Madsen 1987). All these studies focused on relatively large predators, but the consistence of modeling clay is soft enough to register the marks done by insect's mandibles and stings (see Chaves 1998, Pinto 1997, Schwartz 2001), being useful to our purposes.

Spider models were manufactured without legs, simulating the resting position of both *Cyclosa* species. They had about the same size of adult females of *Cyclosa morretes* and were just slightly larger than *C. fililineata* females. Stabilimenta models were also manufactured with similar dimensions of the natural structures. They were composed by two linear segments of modeling clay placed contiguous to a model of a spider, giving the appearance of a continuous column.

For a first essay, we manufactured 95 spider models and 95 stabilimenta with the same color. Each model was crossed by a thread of transparent nylon, which was attached to the vegetation by the two extremities. Thus, the models remained suspended in vertical position, such as most natural columns. The terminal portions of threads (about 3cm) were covered with the same resin used in the experiment 1, to prevent the access of ants. The models remained exposed in the field for 30 days, and then were collected for verification of the marks caused by possible predators of spiders. The one-tailed hypothesis that the frequency of attacks over spider models is higher than over stabilimenta models was tested by the Fisher exact test (Zar 1999).

In the second essay, we manufactured 60 spider models, 60 stabilimenta with the same dark color of the spiders, and 60 white stabilimenta, contrasting with spider's color.

These models also remained in the field for 30 days and then we verified any signal of attack in the artificial spiders and in the segments corresponding to stabilimenta. We used a Chi-square analysis of a 2 (attacked or not) x 3 (white column, dark column or spider alone) contingency table to test if the frequencies of attacks were the same for the three shapes of models. Then, we applied Fisher's exact tests to compare spider models vs. each kind of stabilimenta, and dark vs. white stabilimenta (Zar 1999). The Bonferroni method was used to correct for multiple comparisons (Sokal & Rohlf 1995), considering $\alpha=0.05$.

RESULTS

There was no significant difference between the number of arthropods intercepted by the artificial webs containing stabilimentum of *Cyclosa morretes* and those without this structure ($\overline{X}_{\text{with}} \pm sd=11.5 \pm 4.4$, $\overline{X}_{\text{without}} \pm sd=11.1 \pm 3.6$, $n=10$, $t=0.30$, $p=0.77$). During the five days of exposition 225 potential preys were captured, 115 in the webs with stabilimentum and 110 in the webs without the stabilimentum. The difference in cumulative prey biomass was also not significant for both experimental webs ($\overline{X}_{\text{with}} \pm sd=5.22 \pm 3.25$ mg, $\overline{X}_{\text{without}} \pm sd=4.99 \pm 3.30$, $n=10$, $t=0.16$, $p=0.88$). In addition, the prey types were similar in both treatments (Fig. 4.3). Diptera and Hymenoptera were the most common orders intercepted.

The results for *Cyclosa fililineata* presented the same patterns. Webs with and without stabilimentum intercepted, respectively, 84 and 77 potential preys. The mean number of preys intercepted ($\overline{X}_{\text{with}} \pm sd=8.4 \pm 4.3$, $\overline{X}_{\text{withou}} \pm sd\ _{t}=7.7 \pm 2.9$, $n=10$, $t=0.65$, $p=0.53$) and the total biomass of preys were similar in both treatments ($\overline{X}_{\text{with}} \pm sd=3.04 \pm$

3.95 mg, $\overline{X}_{without}\pm sd = 1.71 \pm 0.84$, n=10, t=1.15, p=0.28). Diptera was again the most abundant order (Fig. 4.4).

As the frequencies of choice of each cage were similar for all the tested stabilimenta ($\chi^2=2.88$, df=1, p=0.089, $n_{flies}=50$ for the first stabilimentum of *C. fililineata*, $\chi^2=0.13$, df=1, p=0.715, $n_{flies}=30$ for the second and $\chi^2=0.53$, df=1, p=0.465, $n_{flies}=30$ for the third; and $\chi^2=0.04$, df=1, p=0.841, $n_{flies}=100$ for the first stabilimentum of *C. morretes*, $\chi^2=0.53$, df=1, p=0.465, $n_{flies}=30$ for the second and $\chi^2=0.13$, df=1, p=0.715, $n_{flies}=30$ for the third) we used a heterogeneity chi-square analysis for replicated goodness of fit tests ($\chi^2=1.76$, df=2, p>0.05 for *C. fililineata*; $\chi^2=0.60$, df=2, p>0.05 for *C. morretes*) and calculated the total chi-square ($\chi^2=1.78$, df=1, p=0.182 for *C. fililineata*; $\chi^2=0.10$, df=1, p=0.752 for *C. morretes*) according to Zar (1999). These results suggest that the visual stimulus of the columns of detritus of both species do not represent an attractive to fruit flies.

In the first essay, we found 93 models of spiders and 84 models of stabilimenta after the 30 days of exposition. The missing replicates could not be considered as removal events, since we also did not find the nylon strings connected to the vegetation, and in some cases, even the branches where they were fixed had disappeared. Possibly these losses were a consequence of rainfalls and therefore were not included in the analysis. The frequency of attacks to spider models in this essay was significantly higher than to models simulating stabilimenta (Fisher's exact test p<0.0001). Forty three spider models (46.2%) presented many marks of attack (Fig. 4.5), while only 10 stabilimenta models (11.9%) presented some signal.

The frequencies of attacked models were also not the same for the three categories in the second essay ($\chi^2=13.9$, df=2, p<0.01). Spider models were again the most attacked ones (42.9% presented some signal of attack), followed by dark (20.8%)

and white stabilimenta (13.6%). The analysis pair to pair showed that there was no significant difference between the frequency of attack in white vs. dark stabilimenta (Fisher's exact test, p=0.223), but there was a significant difference between spider models vs. dark (Fisher's exact test, p=0.011) and spider models vs. white stabilimenta (Fisher's exact test, p<0.001). All the marks, except one, were found in the segments of the stabilimenta molded in spider shape (Fig 4.5D).

DISCUSSION

The comparison between the number of potential preys intercepted by webs with and without stabilimentum showed that structures containing detritus do not improve the prey interception frequency in the studied species. This is the expected result considering that diptera (at least *Drosophila melanogaster* used in our laboratory experiment), the most common prey type intercepted by the artificial webs, seems to be indifferent to the visual sign of a detritus column. These results contrast with those obtained by Watanabe (1999) studying the silk stabilimenta of *Octonoba sybotides* (Uloboridae). He showed that, under light containing short wavelengths, *D. melanogaster* is more likely to choose the direction of a recipient containing a silk stabilimentum. The attraction of diptera to cages with silk stabilimenta was also reported by Craig & Bernard (1990), using two *Drosophila* species and stabilimenta of *Uloborus glomosus* (Uloboridae), and by Bruce *et al.* (2001), using *Chrysomya varipes* (Calliphoridae) and decorated webs of *Argiope keyserlingi* (Araneidae). On the other hand, and also contrasting to our results, Blackledge & Wenzel (2001) tested the prey attraction hypothesis in a field experiment and observed that webs of *Argiope aurantia* without stabilimenta caught more flies than webs containing such structure.

The prey attractive hypothesis is based in UV light reflection properties of the silk stabilimenta (see Craig & Bernard 1990). The addition of detritus over an attractive silk structure is puzzling, since it probably would reduce its effectiveness. In fact, Zschokke (2002) analyzed the UV reflectance of the stabilimenta constructed by four *Cyclosa* species and found that the detritus structures does not show a higher brightness under UV light when compared with white light. For one species, *C. turbinata*, the stabilimentum containing egg sacs had a negative UV-brightness value, indicating that the brightness was higher under white light. This confirms that the reflective properties of detritus stabilimenta are not suitable to attract pollinating insects searching for flower resources or to simulate open areas, as proposed for silk stabilimenta (see Craig & Bernard 1990).

Although *C. morretes* and *C. fililineata* also build other kinds of stabilimenta, including linear and spiral silk structures, the linear stabilimentum containing detritus is the most common type. These spiders seem to construct silk stabilimenta only when detritus are not available (after web destruction, for example), and remain almost their entire lifetime in webs containing detritus (Gonzaga & Vasconcellos-Neto, in prep.). The absence of a relation between the final pattern in the process of stabilimentum construction (detritus column) and prey capture, indicate that these structures probably have evolved through the action of a distinct selective pressure. However, it's possible that the changes during stabilimenta construction, from a silk band to a detritus column, represent a switch between a strategy that improve prey interception to another designed to reduce the risk of predation, and additional experiments involving *Cyclosa* silk stabilimenta are still necessary. An evidence against this hypothesis was provided by Eberhard (2003), studying the construction of stabilimenta in *Allocyclosa bifurca* and *Cyclosa monteverde.* He noted that the experimental addition of egg sacs and detritus stabilimenta to webs lacking these structures inhibited the construction of silk stabilimenta. If the motivation for the construction of a silk stabilimenta is a poor nutritional condition, this procedure would not be effective.

If detritus stabilimenta are not especially attractive nor represent a visual stimulus used by insects to avoid webs, they certainly are more conspicuous (at least to human eyes) than spiders. The association of web decorations with prey location by predators of spiders is often pointed as an argument against the possible protective function of these decorations (Craig *et at.* 2001, Herbestein *et al.* 2000a, Robinson & Robinson 1970, Seah & Li 2001). Seah & Li (2001) demonstrated that *Portia labiata*, an araneophagic salticid that preys on *Argiope versicolor*, is capable of learning to associate the form of the stabilimentum constructed by these spiders with food. In a choice experiment in laboratory, *P. labiata* chose to invade webs with familiar kinds of stabilimenta in a higher frequency than webs with unfamiliar forms. Bruce *et al.* (2001) used this same approach and observed that *Archimantis latistylus* (Mantodea, Mantidae) showed a significant preference over decorated webs. Both experiments, however, were restricted to laboratory. The extrapolation of these results to field conditions depends on some assumptions. First, that these structures are recognizable by predators contrasting with the natural background patterns of colors and brightness. This assumption is dependent, of course, on the visual acuity of predators and on the stabilimenta shapes and composition. Besides, the frequency of encounters between predators and spiders that build stabilimenta should be high enough to allowing the learning that the presence of decorations is associated with food. These aspects must be better investigated in field situations.

Our results concerning spider and stabilimentum models suggest that predators are not capable to associate the shape of a detritus column with a spider. Spider models were much more attacked, and even the addition of columns with a very contrasting color was efficient to reduce the incidence of attacks. It's an indicative that white silk structures could act in the same way of detritus columns, breaking the outline of spider's bodies. We can not be sure if the marks registered in our models were promoted by predators that effectively include *Cyclosa* in their diets. However, if the relatively small and less conspicuous spider models were attacked in a higher frequency, we can suppose that some predatory species are actively searching for prey items with approximately the shape of a *Cyclosa* body. Moreover, It is possible that these predators are failing in identify the stabilimentum as a sign that indicates the presence of resources.

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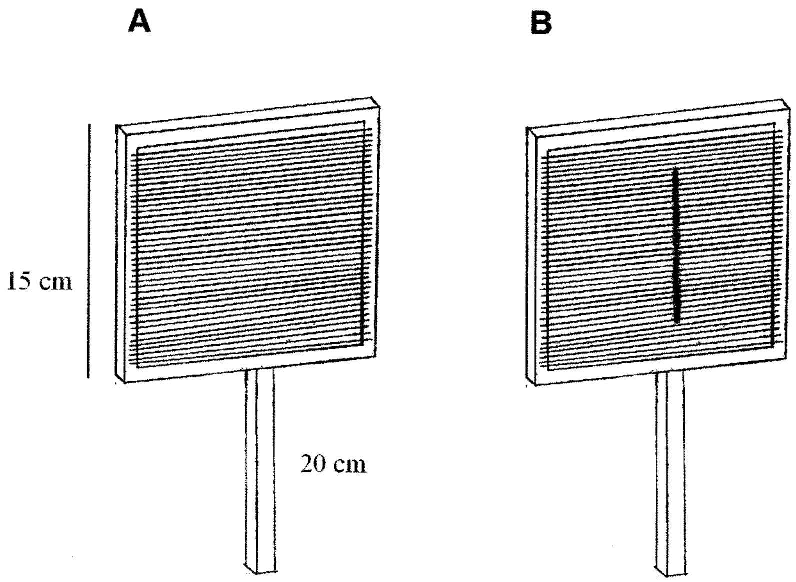


Fig. 4.1: Models of artificial webs. (A) Without stabilimentum, and (B) with a linear stabilimentum attached.

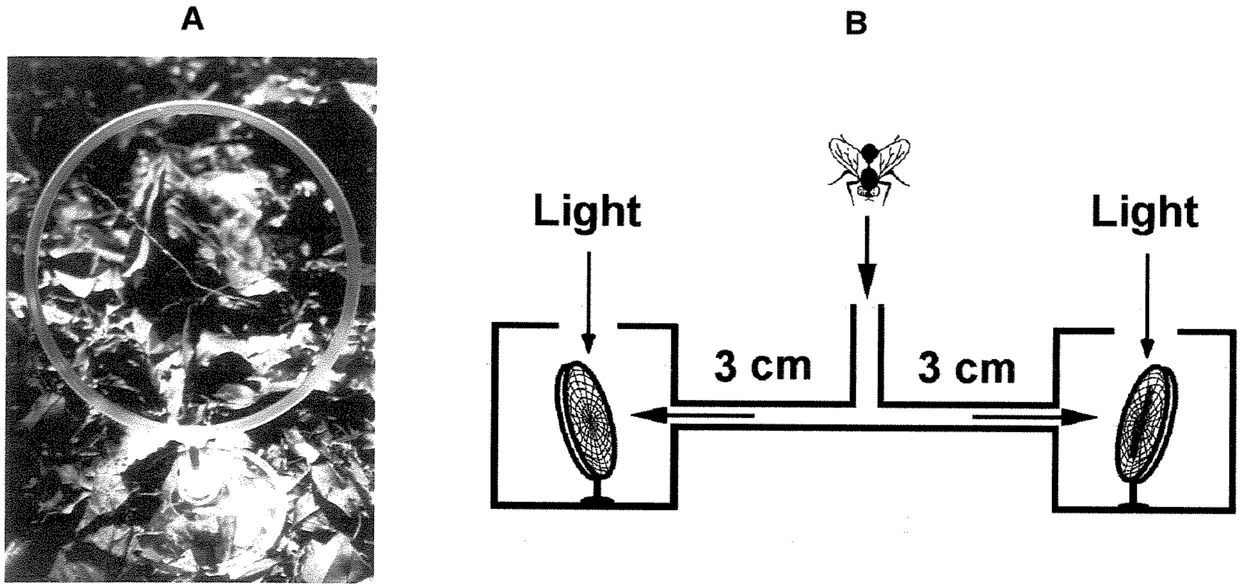


Fig. 4.2:. (A) Plastic ring with a stabilimentum attached, and B) the apparatus used in the choice experiment in laboratory.

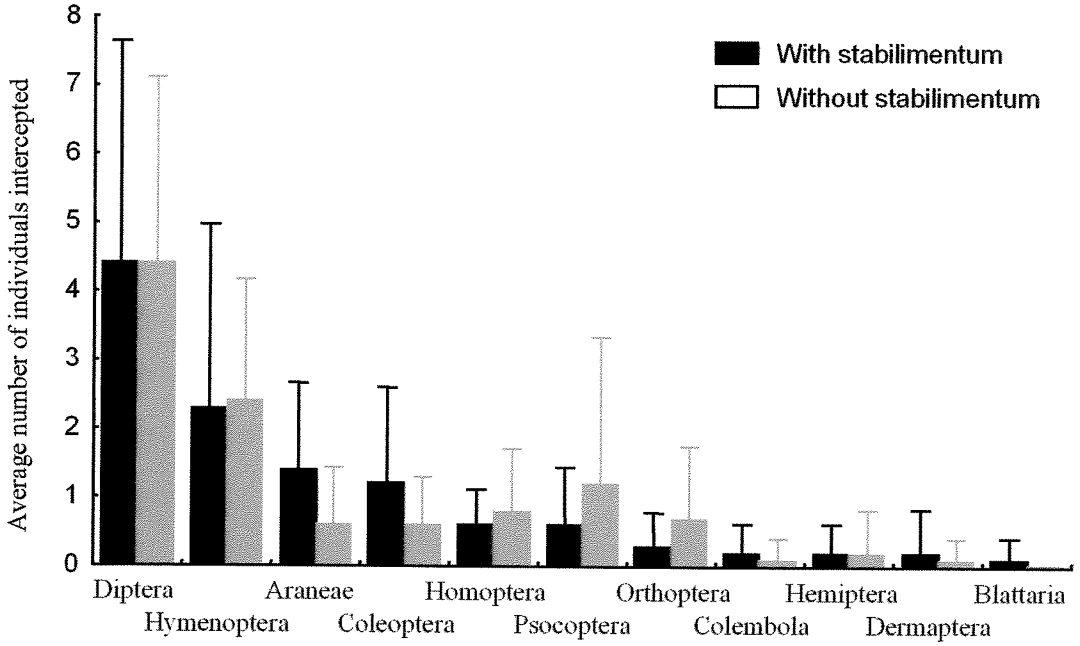


Fig. 4.3: Average number of individuals from each order intercepted per day during the five days of exposition using stabilimenta collected in webs of *Cyclosa morretes.*

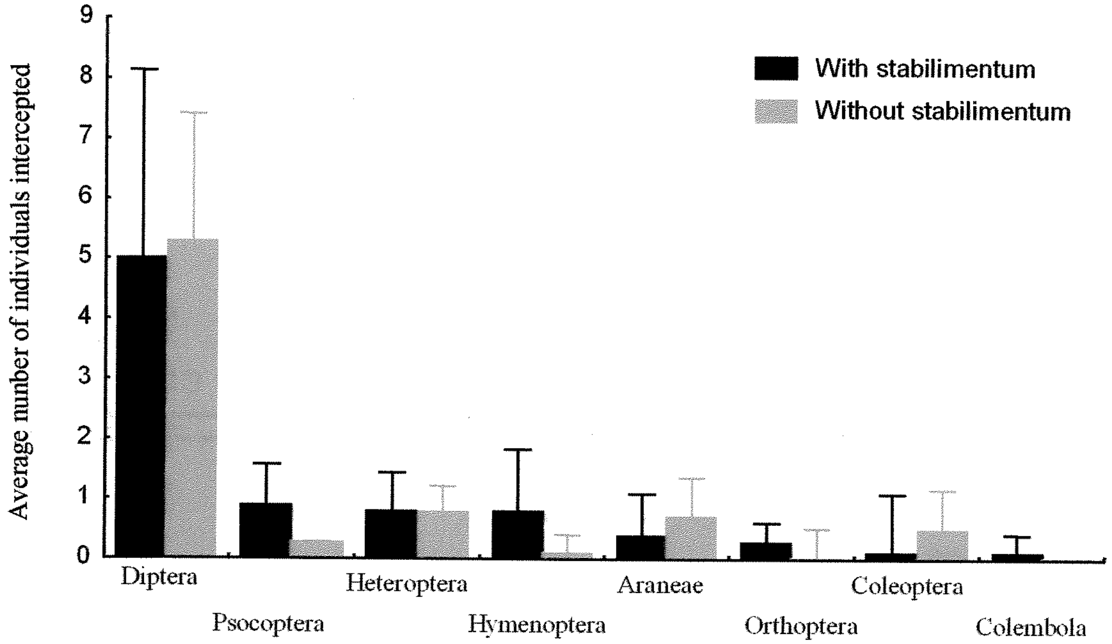


Fig. 4.4: Average number of individuals from each order intercepted per day during the five days of exposition using stabilimenta collected in webs of *Cyclosa fililineata.*

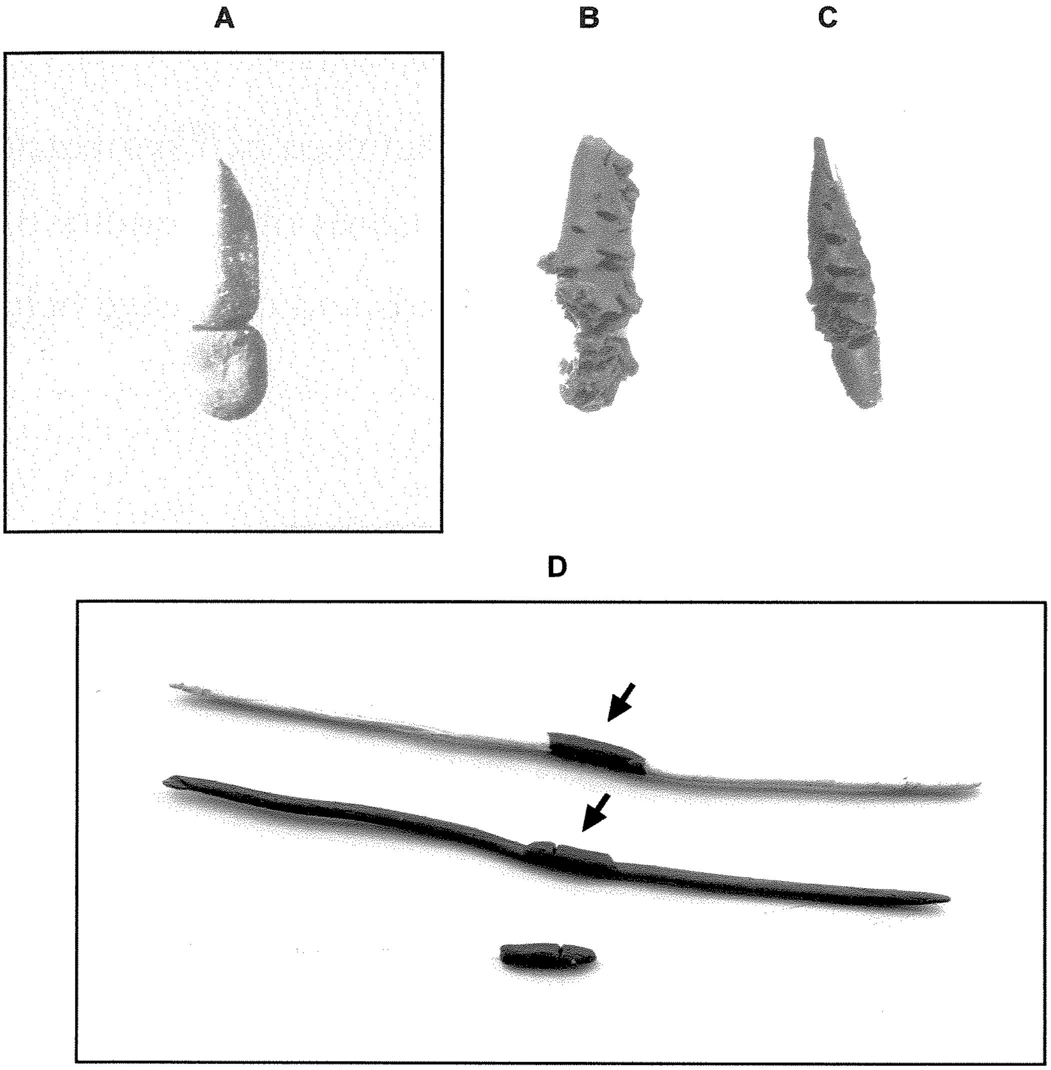
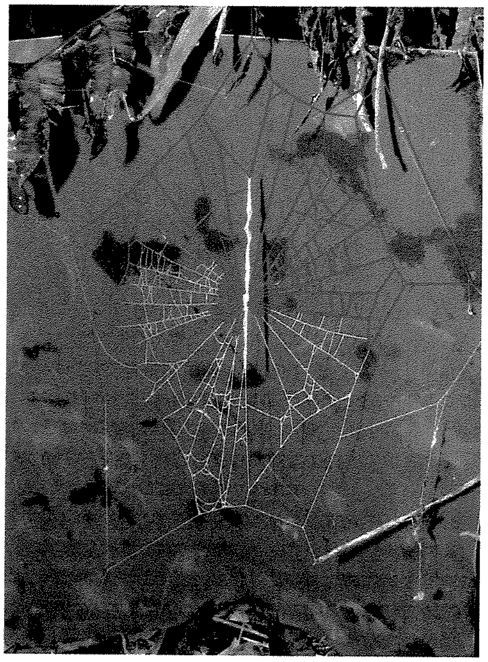


Fig. 4.5: Models of spiders and stabilimenta built with modeling clay. (A) Spider model intact, (B) and (C) spider models presenting marks of attack, and (D) three kinds of models used in the second essay: white and dark stabilimenta models and spider model. The arrows indicate the placement of most attacks in stabilimenta models.

Capítulo 5

Differences in population size between two sympatric *Cyclosa* (Araneae: Araneidae) species: an analysis of fecundity parameters, mortality promoted by parasitoids and defensive behaviours



DIFFERENCES IN POPULATION SIZE BETWEEN TWO SYMPATRIC *CYCLOSA* (ARANEAE: ARANEIDAE) SPECIES: AN ANALISIS OF FECUNDITY PARAMETERS, MORTALITY PROMOTED BY PARASITOIDS AND DEFENSIVE BEHAVIOURS.

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Running title: Differences in population size between two sympatric *Cyclosa*

ABSTRACT

In this study we evaluated the difference in the abundance of two congeneric species of orb-web spiders in an area of Atlantic Forest in Southeastern Brazil, relating this variable to fecundity parameters and frequency of attacks by parasitoids. We also investigated how each species responded to vibrational stimuli, simulating the approximation of a wasp. *Cyclosa fililineata* presented a higher abundance during all the year, although this species produces a lower number of egg sacs and a lower number of eggs per egg sac when compared with *C. morretes*. Both *Cyclosa* species showed similar behavioural responses to vibrational stimuli, but the frequency of the category "keeping motionless" was higher for *C. fililineata*. The frequency of attacks by the wasp *Polysphincta* sp. (Hymenoptera, Ichneumonidae) on adults and juveniles was low and

similar for *C. fililineata* and *C. morretes* in both, dry and wet seasons. This parasitoid species promotes progressive alterations on the web design of their hosts during the growth of the larvae. Webs constructed by spiders with a large larva attached to their bodies presented a lower number of radii and the sticky spirals were completely absent. The parasitoid of eggs, *Baeus* sp. (Hymenoptera, Scelionidae) attacked *C. morretes* more often than *C. fililineata*, possibly as consequence of its higher clutch size and/or larger eggs. These results indicate that egg mortality promoted by *Baeus* sp., but not juvenile and adult mortality promoted by *Polysphincta* sp., may be an important factor determining the relative abundance of these two *Cyclosa* species. However, only the attack by parasitoids can't explain why *C. fililineata* is much more abundant in the studied area.

INTRODUCTION

The impact of vertebrate predators on web-spider populations showed to be significant in several localities, often reducing the density of some species and even the local richness (see Gunnarsson 1998, Rypstra 1984, Schoener & Toft 1983, Spiller & Schoener 1998). The comparison of enclosures from which lizards had been removed with control enclosures with lizards, for example, showed that these predators are able to reduce the abundance of the dominant spiders and exclude some rare species in an island in Bahamas (Spiller & Schoener 1988, 1998). Studies assessing the effects of invertebrate predators and, especially, parasitoids on spider species abundance are much rarer. Some evidence from recent studies, however, suggest that these effects are far from being negligible. Polis *et al.* (1998), for example, found a high decline (of about 77%) in spider densities on desert islands in Gulf of California associated both, temporally and spatially, with increases in the populations of parasitoid wasps (Hymenoptera, Pompilidae).

Hunting-wasps of the families Pompilidae and Sphecidae prey on a large range of web-builders and cursorial species (O'Neil 2001). Unlike vertebrate generalist predators, however, most species of these parasitoids capture preferentially some spider genera or species to provide food for their larvae (see Gonzaga & Vasconcellos-Neto, in prep.). Although a very limited number of studies present data on preferences of other kinds of spider parasitoids, such as ichneumonids, encyrthids and scelionids, many of them were registered using exclusively one or few spider species (e.g. *Hymenoepimecis argyrophaga* - Ichneumonidae which is a parasitoid of *Plesiometa argyra* - Tetragnathidae - Eberhard 2001), suggesting an also high selectivity.

In some spider populations the incidence of parasitism by ichneumonids on adult females can be as high as 30% (Fincke *et al.* 1990). In addition to this mortality factor, their egg sacs can be attacked by a great diversity of egg predators and parasitoids. *Nephila clavipes* (Tetragnathidae), for example, was observed being heavily attacked by *Hymenoepimecis* sp. in Barro Colorado Island, Panama (Fincke *et al.* 1990), and all the fifteen egg sacs of this same species collected by Barnes *et al.* (1992) in Mexico yielded egg predators and/or parasitoids. These high frequencies of parasitism and the selection of specific prey types by invertebrate spider enemies may influence the relative abundance of each species in the field.

Gonzaga & Vasconcellos-Neto (in prep.) investigated prey preferences of Sphecidae species in an area of Atlantic forest in Southeastern Brazil. Relatively rare species of orb-web spiders collected by the authors using visual search surveys were captured in abundance by the wasps. On the other hand, two *Cyclosa* (Araneidae) species, *C. fililineata* and *C. morretes*, showed a high abundance in these surveys, but were completely absent in wasp's nests. Previous studies in other areas, however, showed that, although also ignored by sphecids and pompilids, these *Cyclosa* species are attacked by ichneumonids and by parasitoids of eggs (M.O. Gonzaga, unpublished data).

In this study we compare the relative abundance of *C. fililineata* and *C. morretes* in Parque Estadual Intervales, considering the frequency of attacks by parasitoids and spider's fecundity parameters. We also tested the reactions of both species to artificial vibrational stimuli in order to identify possible differences in their behavioural responses to predators.

MATERIAL AND METHODS

Organisms and study area

Field work was carried out in Parque Estadual Intervales, a forest reserve with about 49,000 ha situated close to Ribeirão Grande (24°16'S; 48°25'W), state of São Paulo, Brazil. All the surveys were performed in an area known as "Carmo".

Cyclosa fililineata is a widespread species, occurring from Panama to northern Argentina. It is smaller than most species of *Cyclosa* (total body length of adult females varying from 3.4 to 5.2 mm) and was previously collected in many distinct habitats, such as Amazonian rainforest (in canopy and close to the soil), gallery forest in Northern Mato Grosso (Levi 1999), Atlantic Forest along several localities of the Brazilian coast, restinga vegetation in São Paulo, and even in very disturbed areas, as eucalypt plantations (M.O. Gonzaga, unpublished data). *Cyclosa morretes* is a little larger (body length of females varying from 5.0 to 7.8 mm) and, except by a female collected in Belém, state of Para, all the registers are distributed from Southeastern Brazil to Northern Argentina. These species were previously collected by the authors in six areas in the states of São Paulo, Minas Gerais and Rio de Janeiro. Both include detritus stabilimenta in their webs, resting during all the time in the hub of the orbs, in a cryptic position. The egg sacs are inserted in the inner space of the column of detritus (Fig. 5.1), and each column can contain multiple egg sacs.

Relative abundance of *Cyclosa* species

We used two methods to evaluate the relative abundance of *Cyclosa morretes* and *C. fililineata* in the study area. The first method was part of a broader study, initially designed to evaluate prey availability for hunting-wasps (see Gonzaga & Vasconcellos-Neto, in prep.). We collected the first 100 orb-web spiders located by visual search from the soil to a height of about 2 m, in river margins, forest borders and in secondary trails. This procedure was repeated every month during one year, from December 2001 to November 2002. In the second method we search specifically for *Cyclosa* webs, registering the species and the type of stabilimenta (linear continuous with detritus, dots of detritus, complex shape with detritus, silk spiral and linear with silk - see Gonzaga and Vasconcellos-Neto, in prep. for additional details on types of stabilimenta) for each individual located. *Cyclosa morretes* and *C. fililineata* can be easily distinguished in the field due to their different body shapes. This procedure was first carried out during the dry season (in July 2003) and then repeated in the wet season (in December 2003).

Fecundity parameters

We collected the first 41 stabilimenta of *C. fililineata* and 39 of *C. morretes* containing egg sacs found in the forest border during the wet season of 2002. The silk present in the detritus stabilimenta and egg sacs were dissolved with 5% sodium hypochlorite (according to the technique suggested by Vetter *et al.* 1996). The eggs contained in each egg sac were counted and 10 eggs were selected randomly to be measured (to the nearest 0.01 mm) using a dissecting microscope with an ocular micrometer. The average egg size for each egg sac was considered as a replicate. In stabilimenta containing more than one egg sac we calculated the average egg size for each egg sac and then the average egg size for the stabilimentum. This last value was considered as a replicate. The same procedure was applied for the egg number.

Comparisons between species were performed by t-tests or Mann-Whitney U-tests. Data normality was checked by Shapiro-Wilks' test (calculated by the program BioEstat 3.0 - Ayres *et al.* 2003) and the homogeneity of variances was checked using the Levene´s test (see Milliken & Johnson 1984). Data was transformed to $\log_{10}$ for application of parametric analysis when deviate from the requirements of normality and homoscedasticity.

Defensive behaviours

To test the behavioural response of *C. fililineata* and *C. morretes* to the approximation of a possible predator or parasite we used the vibrational stimuli promoted by a diapason placed close (0.5 cm) to the web hub. As the abundance of spiders with silk stabilimenta and with discontinuous detritus structures was relatively low (see Gonzaga & Vasconcellos-Neto, in prep.), we used only spiders with stabilimenta composed by detritus in a linear continuous shape. The vibrating diapason was slowly moved toward the spider, simulating a direct attack, and its reaction was registered. This procedure was repeated with 371 females of *C. fililineata* and with 102 females of *C. morretes*. Comparison between the frequency of behavioural categories on both species was performed by a chi-square analysis of contingence table (Zar 1999).

Natural enemies

We evaluated the frequencies of attacking of two kinds of natural enemies: parasitoids of eggs and parasitoids of juveniles and adults. The occurrence of parasitoids of eggs was evaluated using the same egg sacs collected for the estimative of fecundity parameters. The frequency of adult and juveniles attacked by ichneumonids was estimated by the inspection of 1222 spiders, 787 in the dry season and 435 in the wet season of 2003. The inspections were conducted by visual search following the same trails used for estimative of relative abundance of *Cyclosa* species. The abdominal region of each spider, where the larvae are usually located, was inspected using a 10x hand magnifier.

The webs of parasitized spiders found in the wet season were coated with cornstarch (following Eberhard 1976) and photographed with a digital camera to evaluate changes in web designs among hosts presenting small and large (closer to pupate) larvae. The digital pictures were manipulated with the program Adobe Photoshop (Adobe Systems Inc.) to remove the background.

RESULTS

Relative abundance of two *Cyclosa* species

A higher number of *C. fililineata* individuals was captured in all the monthly surveys. The highest differences between both species were found in the period from May to August (Fig. 5.2), in the dry season, when we collected a great number of immature individuals of *C. fililineata*. The predominance of *C. fililineata* was confirmed by the method of specific search in 2003, but in these samples we observed a greater difference in

December (wet season). In the surveys conducted in the dry season we found a total of 193 individuals of *C. morretes* and a number three times higher of *C. fililineata* (594 individuals). In the wet season we found 50 individuals of *C. morretes* and 385 of *C. fililineata*.

Fecundity parameters

The mean number of egg sacs produced by each female of *C. morretes* was higher than the number produced by *C. fililineata* ($\overline{X}_{C.morretes}$±sd =3.62 ±1.20, n=41 stabilimenta; $\overline{X}_{C.fililineata}$±sd =2.73±1.77, n=39 stabilimenta, Mann-Whitney U = 561.50, p=0.022). In addition, the number of eggs per egg sac ($\overline{X}_{C.morretes}$±sd = 29.7±12.2, n=41 stabilimenta; $\overline{X}_{C.fililineata}$±sd =12.9±4.2, n=39 stabilimenta; t-test, t=-9.01, p<0.001) and, consequently, the total clutch size of *C. morretes* was also higher ($\overline{X}_{C.morretes}$±sd =115.9±76.5 eggs per female, n=36 females; $\overline{X}_{C.fililineata}$±sd =34.0±17.3 eggs per female, n=39 females; t-test, t=6.52, p<0.0010). Finally, the females of *C. morretes* also produced larger eggs ($\overline{X}_{C.morretes}$±sd =0.65±0.04mm, n=36 females; $\overline{X}_{C.fililineata}$±sd =0.60±0.04mm, n=36 females; t-test, t=-4.84, p<0.001).

Defensive behaviours and natural enemies

Reactions to vibrational stimuli

Four categories of behaviours were observed after the approximation of the vibration source:

(1) Attacking: The spiders try to reach the stimulus with their anterior legs and sometimes pull some web strings.

(2) Running: The spiders run away from the hub with a range of distances varying from few centimetres to the web periphery.

(3) Jumping: The spiders drop down to the ground or vegetation along a drag line and stay motionless, generally returning to the hub of the web few minutes later.

(4) Keeping motionless: The spiders keep their position in the stabilimentum, sometimes retracting the legs close to their bodies.

The frequency of these behavioural categories was different between species (χ^2 =10.17, d.f.=3 , p=0.017). This difference is specially related to the higher frequency of the category "keeping motionless" in *C. fililineata* (Fig. 5.3). Excluding data for this category and considering just the remaining 2 x 3 contingency table supports the hypothesis that the frequencies of categories 1, 2 and 3 are the same between species (χ^2=0.37, d.f.=2 , p=0.832).

Parasitoids of juveniles and adults

Both species were attacked by *Polysphincta* sp. (Hymenoptera, Ichneumonidae, Pimplinae) (Fig. 5.4). The frequency of parasitism by this wasp was low and similar for both *Cyclosa* species in dry season (χ^2 =0.24, d.f. = 1, p=0.62) and in wet season (χ^2 =1.06, d.f. = 1, p=0.30) (Table 5.1). We did not witness the wasps attacking spiders, but on one occasion a female of *C. fililineata* was found on the vegetation, below the web position, while a wasp was resting at the web hub. The spider may have reacted to the wasp approximation jumping to vegetation, and the wasp took its position, waiting for another opportunity to attack.

The webs constructed by spiders with young larvae attached to their bodies seems to keep all the characteristics (number of radii, spirals, diameter and symmetry) of webs constructed by unparasitized spiders. The number of parasitized spiders sampled, however, was too small for statistic analysis. In spite of that, the comparison of webs build by spiders carrying larvae with different sizes clearly indicate a progression towards the reduction of radii threads and elimination of spirals during larva development (Fig. 5.5).

Parasitoids of eggs

Eggs of both *Cyclosa* species were parasitized by *Baeus* sp. (Hymenoptera, Scelionidae), a small wingless wasp adapted to burrowing through the silk layers of spider's egg sacs. The frequency of attacks by *Baeus* sp. on stabilimenta was greater in *C. morretes* (39.1% of 46 stabilimenta analysed) than in *C. fililineata* webs (5.1% of 39 stabilimenta) ($\chi^2 = 14.37$, d.f. = 1, $p<0.001$). The discrimination between parasitized and unparasitized eggs can be done due to changes in egg coloration and by the identification of some morphological characteristics of the wasps (such as the large pigmented eyes and the antennae) (Fig. 5.6). However, eggs of *Cyclosa* containing just the eggs of *Baeus* sp. or very young larvae are probably undistinguishable from normal eggs. Thus, we probably underestimate the number of parasitized egg sacs for both host species.

The percentage of parasitized eggs within *C. morretes* egg sacs varied from 33 to 100% ($\overline{X}$=78.8%, d.p.=22.7%) and the maximum number of parasitoids found in an egg sac was 46. There is a significant positive relation between the number of eggs in the egg sac and the number of eggs parasitized. This relation, however, is limited by the fecundity capacity of *Baeus* females (Fig. 5.7). In *C. fililineata* we found just one egg sac completely parasitized (10 eggs) and another one containing an adult female of *Baeus*. Considering the total number of eggs produced by each female of *C. morretes*, *Baeus* can destroy from 9 to 100% of the clutch ($\overline{X}$=36.7%, d.p.=29.6%).

DISCUSSION

Although absent in the nests of two species of hunting-wasps in P.E. Intervales (Gonzaga & Vasconcellos-Neto, in prep), *C. fililineata* and *C. morretes* are attacked by at least two parasitoid Hymenoptera, *Polysphincta* sp. and *Baeus* sp. The frequency of attacks by *Polysphincta* was relatively low for both host species (considering the incidence of parasitism by ichneumonids in populations of other hosts - e.g. Fincke *et al.* 1990). On the other hand, *Baeus* sp. was found in almost 40% of the stabilimenta containing egg sacs of *C. morretes*. This proportion was much higher than the frequency of attacks by another unidentified *Baeus* species on populations of *Lepthyphantes tenuis* and *Erigone* spp. (Linyphiidae) in England (Van Baarlen *et al.* 1994).

Host selection by scelionids is a poorly known subject. Studies on the closed related genus *Ceratobaeus*, in Australia, suggested that they use chemical signs provided by both, host and host microhabitat, to find the egg sacs (Austin 1984). It is possible that *Baeus* sp. also use some kind of specific chemical cue to locate *C. morretes*. Preferentially entering in *C. morretes* egg sacs, *Baeus* females find a larger number of eggs available to be used and large eggs, which can provide more food for their larvae. The maximum number of parasitized eggs in an egg sac (46) indicate that *Baeus* sp. females may produce much more eggs than the number usually found in *C. fililineata* egg sacs. In addition, the age of host eggs may restrict their suitability for the parasitoid. Valerio (1984) showed that *Baeus achaearaneus* oviposits more in eggs of intermediate age and less in eggs recently laid (< 18h old). Austin (1984) found that *Ceratobaeus masneri* females never oviposit in eggs older than approximately two days. As *C. morretes* produces a larger number of egg sacs, the probability of finding eggs with the appropriated age for *Baeus* sp. requirements probably is higher for most stabilimenta of this species.

The expressive difference in the relative abundance of both *Cyclosa* species, however, can not be explained just by the mortality promoted by the parasitoids. *Cyclosa morretes* produces a mean number of eggs more than three times superior than the number produced by *C. fililineata*. In spite of that it was less abundant in all samples conducted in 2002 and 2003. A number of other factors can be responsible for this pattern of abundance. A differential predation by other natural enemies (e.g. birds, lizards, mantids), for example, may contribute to a higher mortality of *C. morretes* juveniles. The frequency of discontinuous stabilimenta in the webs of this species is much higher than in juveniles of *C. fililineata*. If these structures (which are an intermediate stage in the process of construction of a continuous stabilimentum - see Gonzaga & Vasconcellos-Neto, in prep.) were less effective in reducing the risks of predation, *C. morretes* individuals could be more exposed during at least part of their lives. Differences in behavioural responses to vibrational stimuli may also contribute to a higher risk of predation by *C. morretes*. Keeping motionless in a higher frequency, *C. fililineata* individuals reveal their position in the middle of detritus less often than *C. morretes*. Another possibility is that these species may be spatially segregated. We may have conducted the samples in an area or vegetation stratum preferentially used by *C. fililineata* individuals.

Webs spun by *C. fililineata* carrying large larvae of *Polysphincta* sp. may indicate a case of host manipulation. The reduced number of radii and absence of stick spirals in the webs probably minimize the risks of insect interception when the parasitoid larvae spins their cocoons. These modifications may also reduce web visibility and, consequently, the risks of attacking by visually oriented predators. Eberhard (2000a, 2000b , 2001) described a change in web design of *Plesiometa argyra* (Araneae, Tetragnathidae) induced chemically by the larvae of *Hymenoepimecis argyraphaga* (Hymenoptera, Ichneumonidae) on the night they will kill the hosts. The spiders repeated specific behavioural sequences several times during web construction, building a strong structure specially suited to constitute a stable platform. These platforms were used by the larvae to attaching their cocoons, reducing the vulnerability of pupae to heavy rains. Our results, however, suggest that web alterations in *Cyclosa* are progressive during larva development, instead of sudden, as happens with *P. argyra*. Thus, the lacking of some web threads may also be the result of a debilitated state promoted by larva feeding during a long time. The confirmation of the manipulative hypothesis still depends on experiments testing the effects of the removal of the parasitoid on host web construction behaviour.

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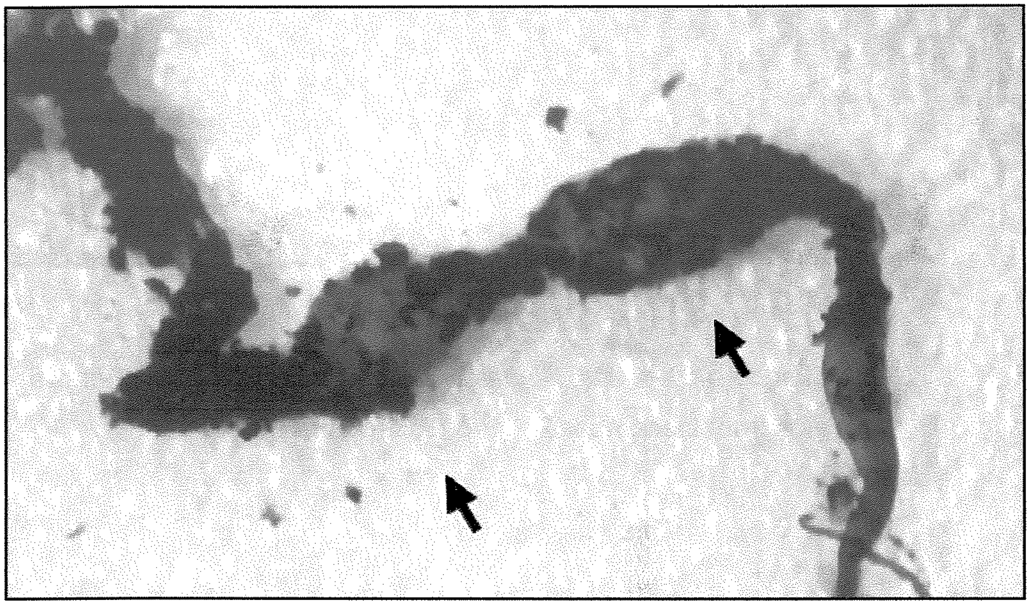


Fig. 5.1: Stabilimentum of *Cyclosa morretes* showing two egg sacs in contiguous positions.

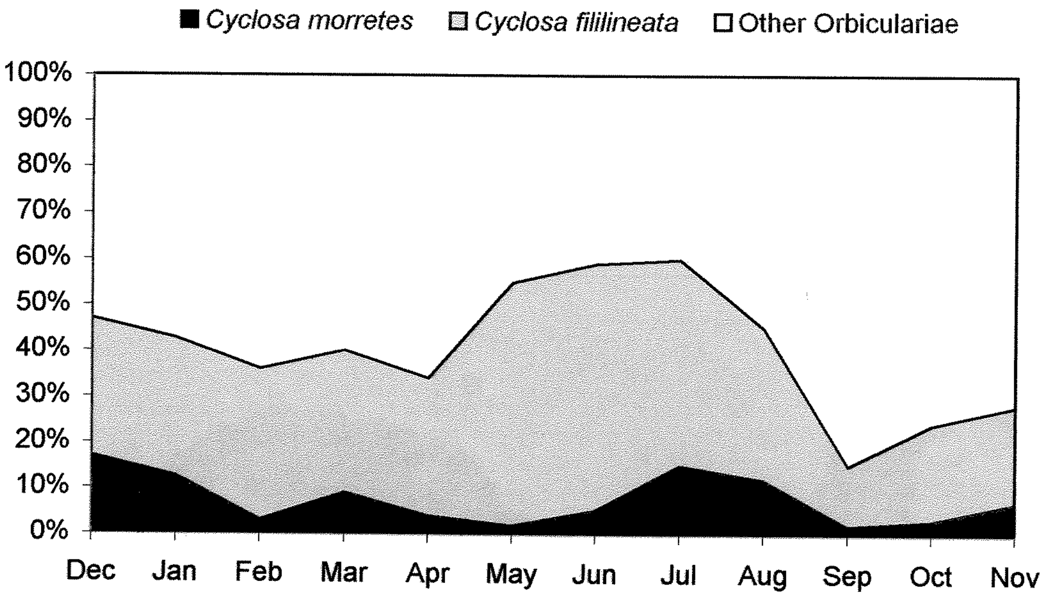


Fig. 5.2: Relative abundance of *Cyclosa fililineata*, *Cyclosa morretes* and other orb-web builders in P.E. Intervales from December 2001 to November 2002.

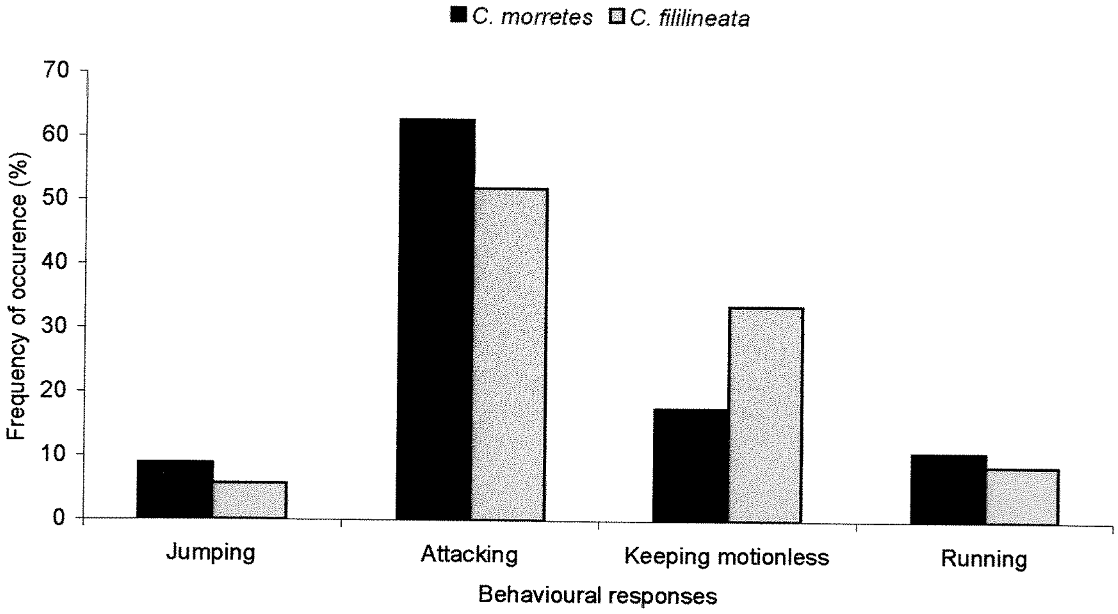


Fig. 5.3: Frequency of each behavioural response after a vibrational stimuli (n=102 for *C. morretes* and n=371 for *C. fililineata*).

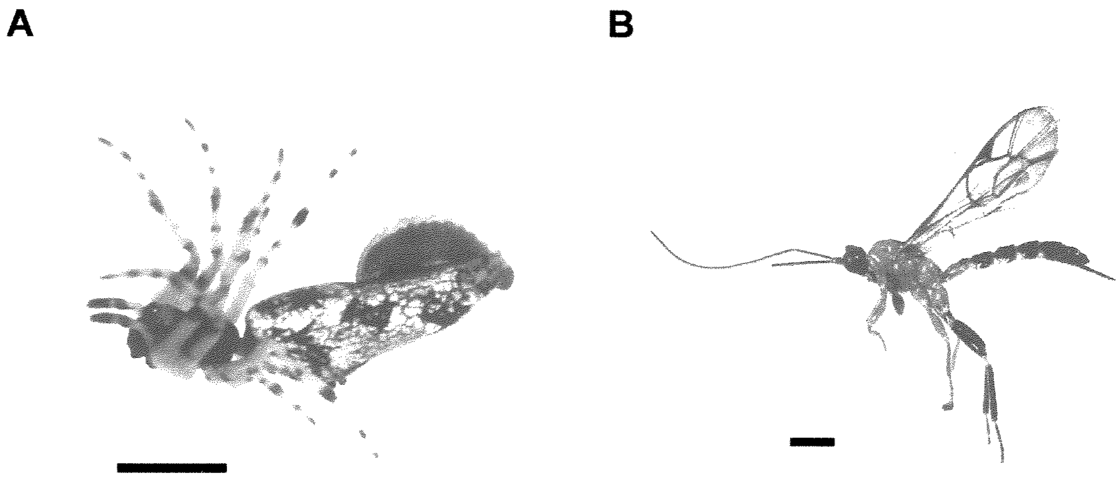
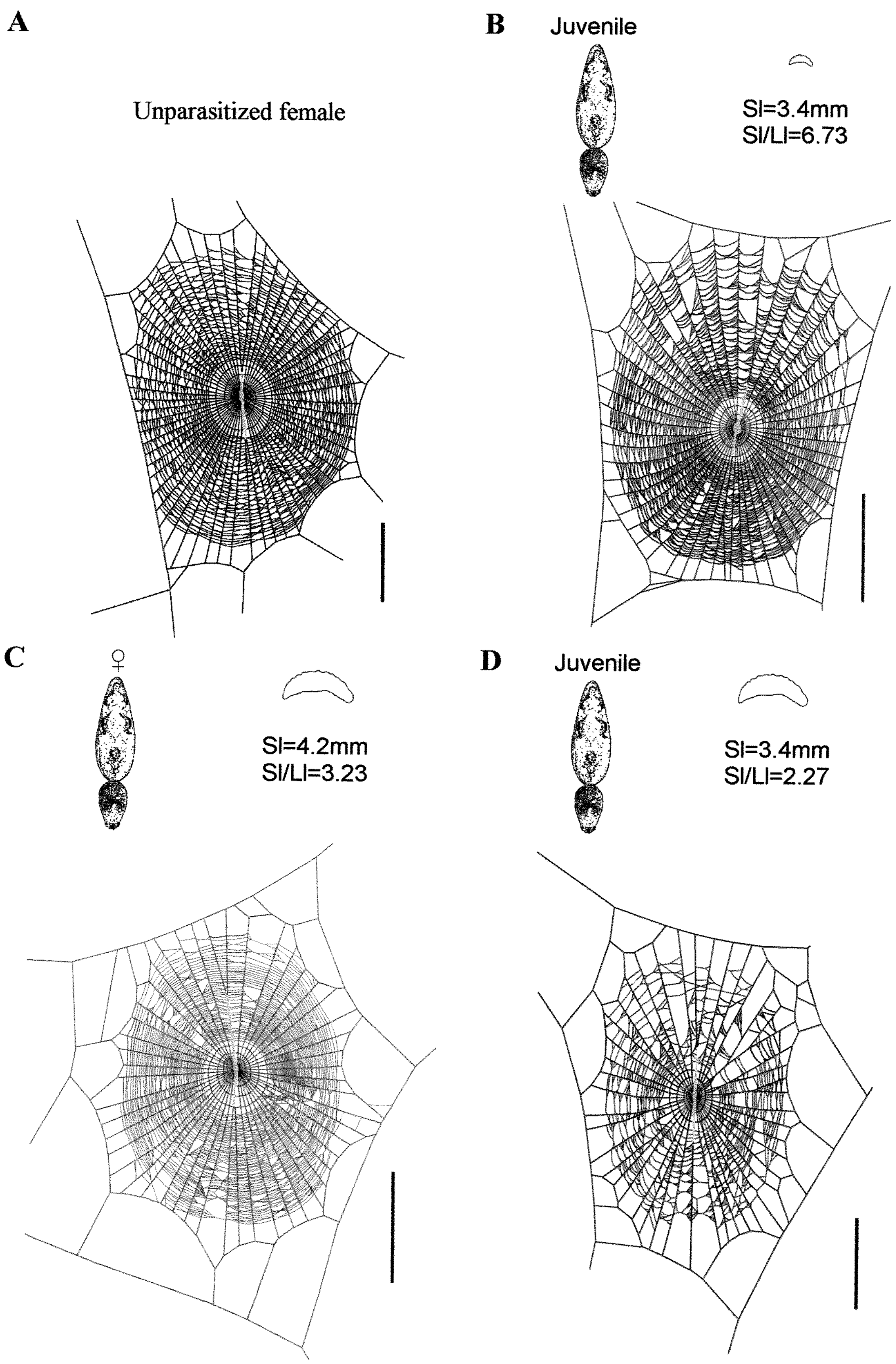


Fig. 5.4: A - *Cyclosa fililineata* with a larva of *Polysphincta* sp. attached to its abdomen. B - *Polysphincta* sp. adult female. Scale bars = 1mm.

Table 5.1: Frequency of parasitism by *Polysphincta* sp. in *Cyclosa morretes* and *C. fililineata* in samples conducted in dry and wet seasons.

		C. morretes		***C. fililineata***	
	Type of Stabilimentum	Unparasitized	Parasitized	Unparasitized	Parasitized
Dry season	Column of detritus	56	1	577	9
	Dots of detritus	132	1	2	0
	Spiral	1	0	0	0
	Linear with silk	2	0	6	0
	Total	**191**	**2 (1.04%)**	**585**	**9 (1.54%)**
Wet season	Column of detritus	42	0	372	8
	Dots of detritus	6	0	1	0
	Spiral	0	0	3	0
	Linear of silk	0	0	1	0
	Complex	2	0	0	0
	Total	**50**	**0 (0%)**	**377**	**8 (2.12%)**


A
Unparasitized female
B
Juvenile
Sl=3.4mm
Sl/Ll=6.73
C
♀
Sl=4.2mm
Sl/Ll=3.23
D
Juvenile
Sl=3.4mm
Sl/Ll=2.27

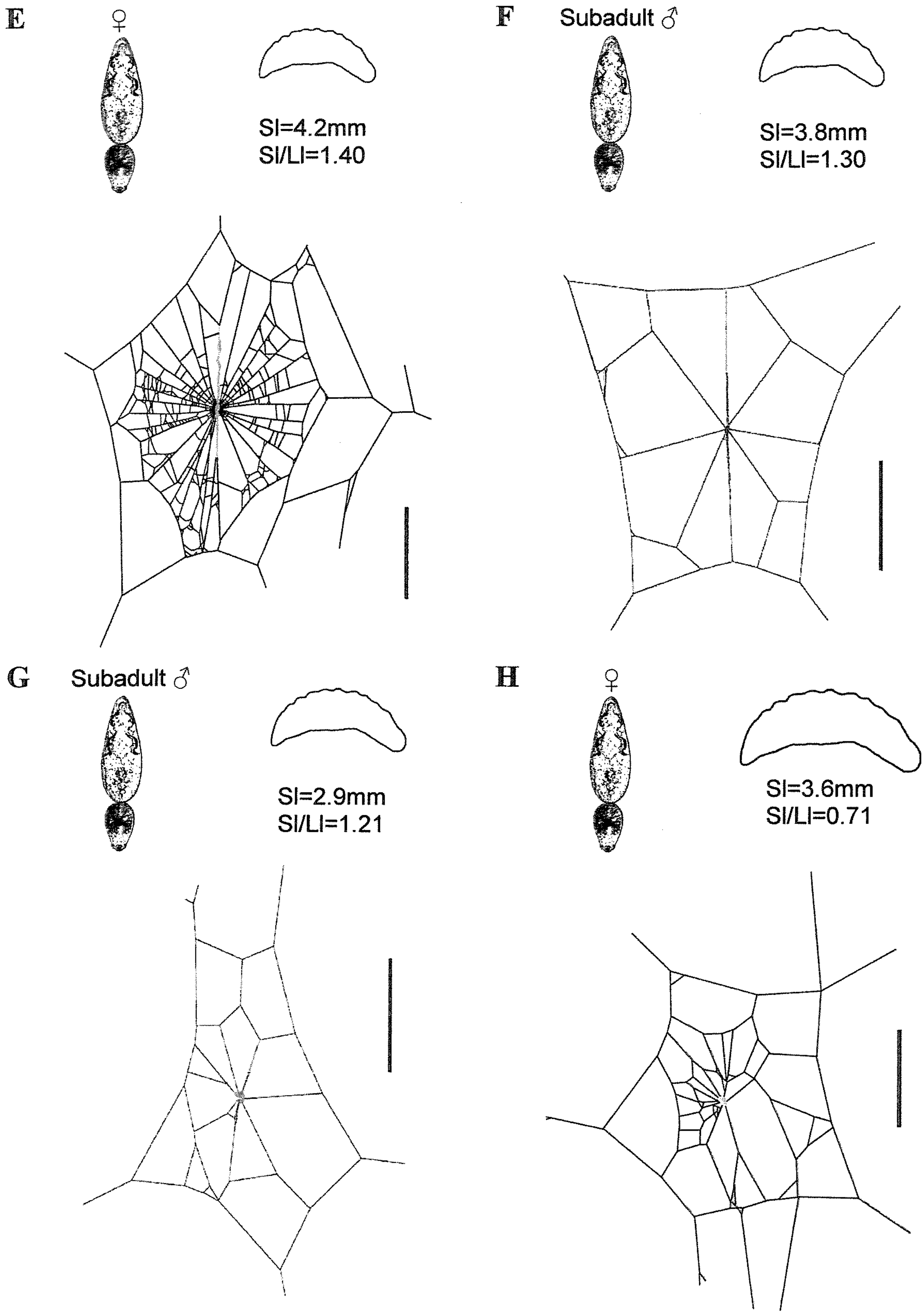


Fig. 5.5: Webs of an unparasitized female and webs of 7 spiders with *Polysphincta* sp. attached to their abdomens. The drawings of the larvae indicate their size in relation to the spider on the left. Sl = Spider body length, Ll= Larva body length. Scale bars = 5cm.

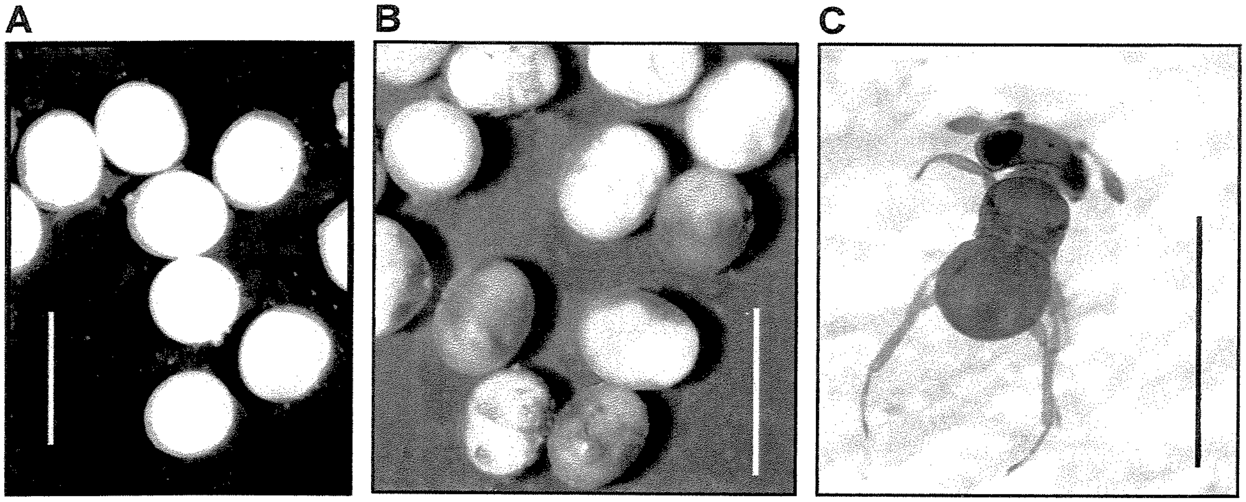


Fig. 5.6: A - Eggs of *Cyclosa morretes*. A- normal eggs, B- eggs with the parasitoid *Baeus* sp., C - Adult of *Baeus* sp. Scale bars = 1mm.

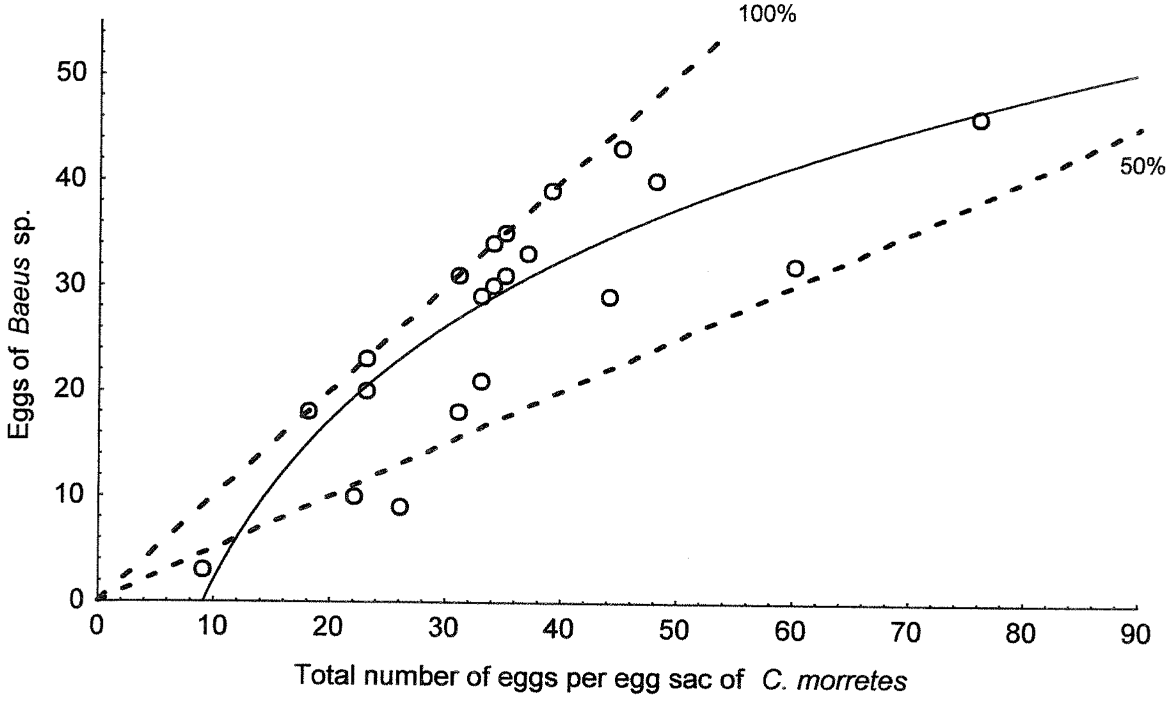
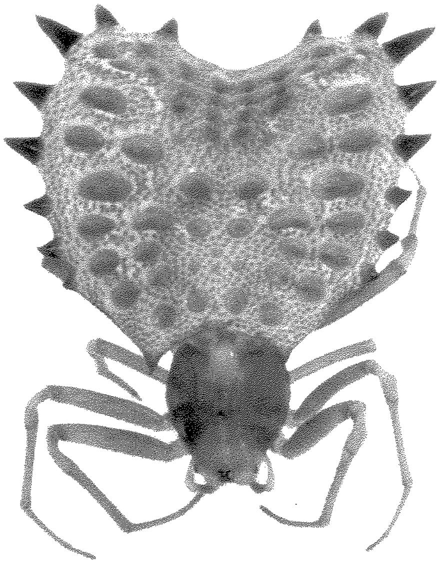


Fig. 5.7: Relation between the total number of eggs in egg sacs of *C. morretes* and the number of eggs parasitized by *Baeus* sp. ($y=-48.34+21.90*\log x$, $r^2=70.02$, d.f.=20, $p<0.001$). The dashed lines indicate the interval between 50% and 100% of parasitism.

Anexo 1

A new species and a new synonymy in the spiny orb-weaver spider genus *Micrathena* (Araneae, Araneidae)



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A NEW SPECIES AND A NEW SYNONYMY IN THE SPINY ORB-WEAVER SPIDER GENUS *MICRATHENA* (ARANEAE, ARANEIDAE)

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Running title: A new species and a new synonymy in *Micrathena*

ABSTRACT. A new species, *Micrathena cicuta*, is described and illustrated based on females from Southeastern Brasil. *Plectana degeeri* Walckenaer is synonymised *with M. plana* (C.L. Koch) based on the original description.

Keywords: Araneae, Araneidae, *Micrathena*, Brasil, South America, systematics.

INTRODUCTION

The genus *Micrathena* Sundevall, 1833 is a common and conspicuous group of diurnal spiders that is endemic to the Americas. It can be easily recognized by their spiny abdomen, vertical orb-webs with an open hub, and their characteristic upside down position on the webs, with the abdomen inclined horizontally. It differs from *Gasteracantha* Sundevall by the shape of carapace and from *Chaetacis* Simon by lacking spines or tubercles on the carapace behind lateral eyes (Levi 1985). The genus was revised by Levi (1985) and comprises 104 species with a mostly Neotropical distribution. Of these, 33 are known only from females, and except for two notes describing males of previously known species (Bonaldo, 1990; Lise, 1995) and by the synonymy of *Thaumastobella mourei* Mello-Leitão, 1945 with *Micrathena saccata* (C.L. Kock, 1836) (Scharff 1991), the systematics of the genus has remained unaltered since Levi's revision.

In this paper we describe a new species, *Micrathena cicuta*, of the *kirbyi* group (as defined by Levi 1985). This is the largest species group in this genus, including 45 species distributed from Central America to Southern South America. Additionally, we synonymize *M. degeeri* (Walckenaer, 1842) with *M. plana* (C.L. Koch, 1836), another member of the *kirbyi* group, based on the original description.

The specimens examined were deposited in the spider collection of the Instituto Butantan, São Paulo (IBSP) and Museu de Zoologia, Universidade de São Paulo (MZSP). The description format follows Levi (1985), and all measurements are in millimeters.

RESULTS

Micrathena cicuta

(Figs. 1-5)

Types.- Female holotype from Volta Redonda, Área de Relevante Interesse Ecológico Floresta da Cicuta, 22°31'S 44°07'W, State of Rio de Janeiro, Brasil, 18.February.2002, M. O. Gonzaga col. (IBSP 36322). Female paratype from Resende, District of Serrinha do Alambari, 22°20'S 44°30'W, State of Rio de Janeiro, Brasil, E.F. Ramos col., 31.March.1996 (IBSP 27195).

Etymology.- The specific name is a noun in apposition taken from the type locality.

Diagnosis.- *Micrathena cicuta* shares with *Micrathena clypeata* (Walckenaer, 1805) a flat abdomen with rounded sides, covered by several sclerotized disks and minute granules and with one anterior pair of spines. It is distinguished by the abdomen with eight marginal pairs of black thorns (five in *M. clypeata*) and by the absence of dimples on the carapace (Fig. 1). The epigynum differs by the narrower lateral lobes and median plate in ventral and posterior views (Figs. 2, 3), the anteriorly notched transverse bar with a longer and posteriorly directed lobe (Fig. 3) and by the rounded bulge in lateral view (Fig. 4).

Description.-Male. Unknown.

Female (holotype). Carapace orange, with a high thoracic region. Clypeus, chelicerae, labium, endites and sternum orange. Palpus and legs orange-brown, darker ventrally. Abdomen orange, lighter than carapace, with one anterior pair of spines overhanging carapace and eight pairs of marginal black thorns. Dorsum of abdomen flat with a slight posterior median longitudinal depression. Dorsal sclerotized disks and minute granules as in *M. clypeata*. Total length 8.6, carapace 2.8 long, 2.5 wide. First femur 2.3; patella and tibia 2.5; metatarsus 1.0; tarsus 0.6. Second patella and tibia 2.3; third patella and tibia 1.4. Fourth femur 3.2; patella and tibia 2.3; metatarsus 1.6; tarsus 0.7.

Distribution.- Known only from Southeastern Brasil. This species seems to be closely related to *M. clypeata*, which occurs along the Panama, Northern South America and Amazon Basin (Fig. 5). These two species display a disjunct distribution, occurring in tropical rainforest areas separated by Central and Northeastern Brazilian savanna vegetations (cerrado and caatinga, Hueck 1972).

Additional material examined.- BRASIL: *São Paulo*: Salesópolis, Estação Biológica de Boracéia, V.2001, equipe BIOTA, ♀ (IBSP 39799); Cotia, Reserva Florestal de Morro Grande, 26.III.2003, A. A. Nogueira *et al.*, 1♀ (IBSP 39794), 4♀ (IBSP, 39795 - 39798); 15♀ (MZSP).

***Micrathena plana* (C.L. Koch)**

Acrosoma planum C.L. Koch, 1836: 81, fig. 228.

Micrathena plana: Levi, 1985: 509, figs. 311-325, map 6.

Plectana degeeri Walckenaer, 1842: 174 (female holotype from Suriname, lost) **New synonymy**.

Acrosoma degeeri: Butler, 1873: 425.

Micrathena degeeri: Petrunkevitch, 1911: 368; Platnick, 2003.

Synonymy – *Micrathena degeeri* was overlooked by Levi (1985), and as occurred to all species described by Walckenaer (1842), the type specimens were lost. According to the original description (Walckenaer, 1842: 174), *M. degeeri* possesses an oval-triangular abdomen with 12 spines: an anterior pair of small ones (described as "médiocre" by the author), a pair of large and diverging posterior spines with two small ones on the base, one dorsal and one ventral. The sides of the abdomen were described as presenting two small spines. This description matches Levi's (1985) illustrations of *Micrathena plana*, a species distributed from Panama and West Indies to Argentina, and the only species with 12 abdominal spines recorded from Suriname. As such, we here consider *M. degeeri* a junior synonym of *M. plana*.

ACKNOWLEDGEMENTS

We are especially grateful to Angela M.F. Pacheco for the illustrations, and Cristina A. Rheims, Ricardo Pinto da Rocha, and André A. Nogueira for providing additional specimens for this study. We are also indebted to Fundação CSN and IBAMA for allowing our studies in the ARIE Floresta da Cicuta. Antonio D. Brescovit, C. A. Rheims, Glauco Machado, and two anonymous reviewers are acknowledged for helpful suggestions on the manuscript. This study was financed by FAPESP doctoral fellowship grants (Proc. 99/06089-4 to M.O. Gonzaga and 99/05659-8 to A.J. Santos).

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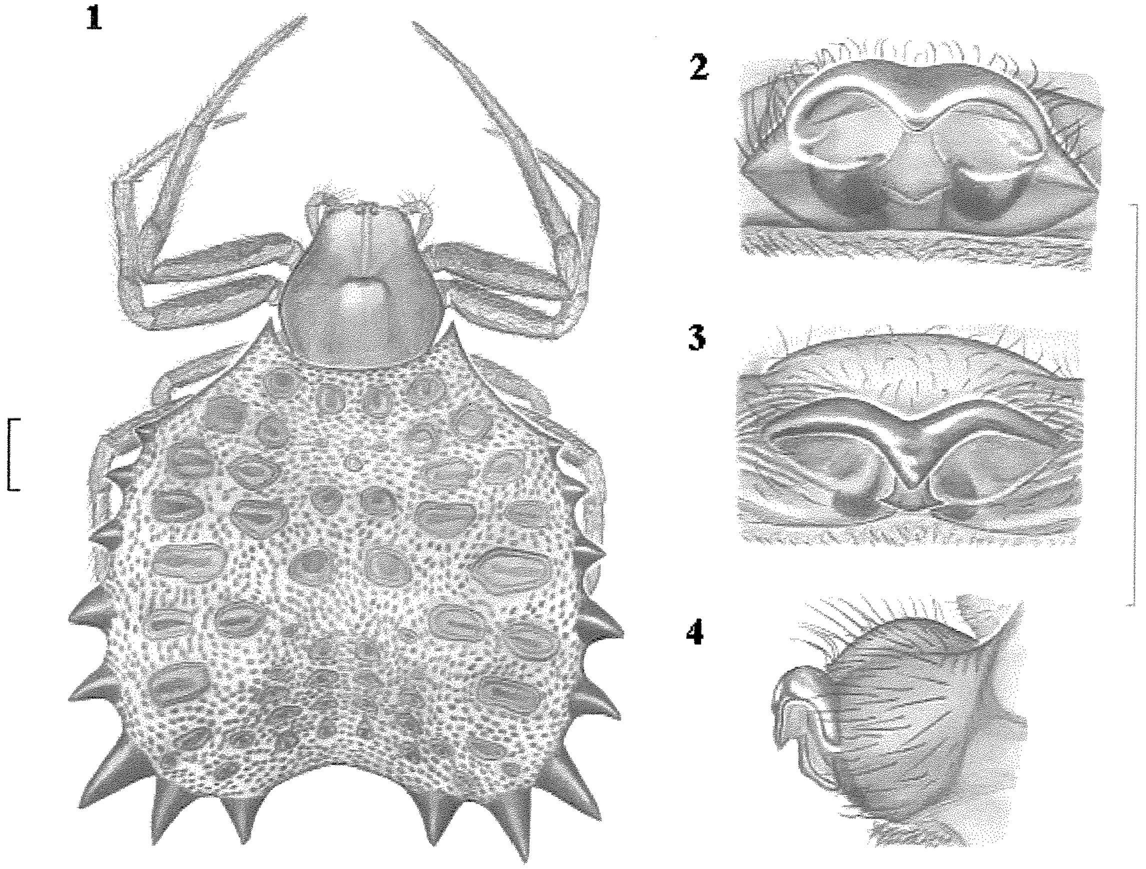


Figures 1-4.- *Micrathena cicuta* new species. 1. Female habitus, dorsal view. 2. Female epigynum, posterior view. 3. Ventral. 4. Lateral. Scale bars, 1 = 1.00 mm; 2-4 = 0.50 mm.

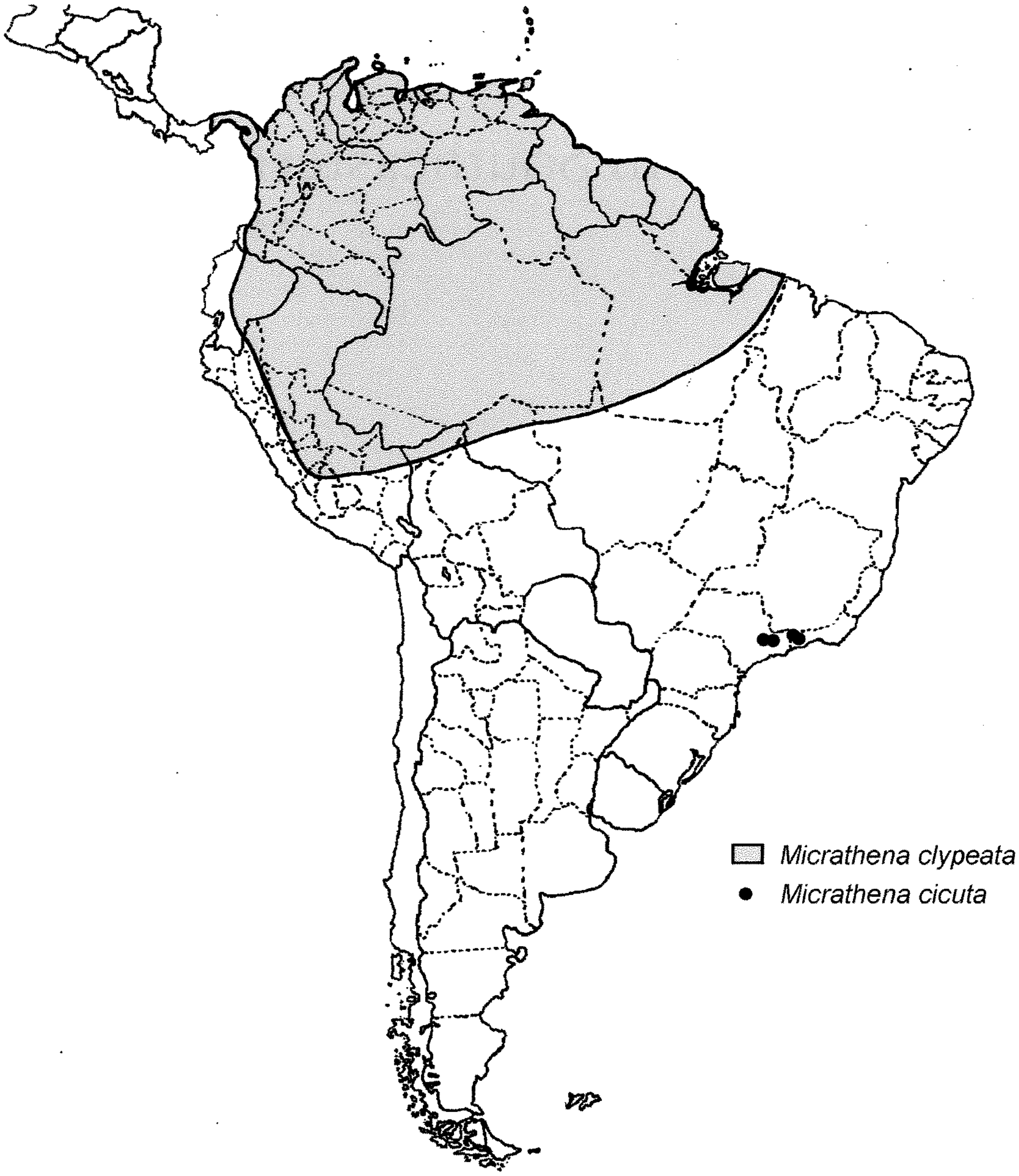
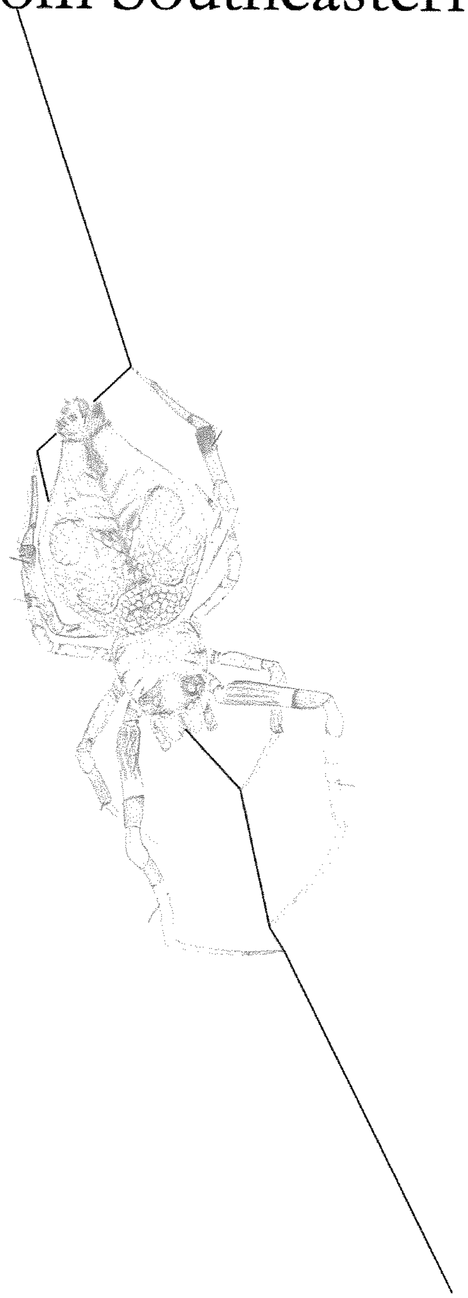


Figure 5.- Geographic distribution of *Micrathena clypeata* (gray area, based on records from Levi, 1985) and locality records for *Micrathena cicuta* new species (dots).

Anexo 2

Sybota demariai (Araneae, Uloboridae), a new species from Southeastern Brazil



SYBOTA DEMARIAI (ARANEAE, ULOBORIDAE), A NEW SPECIES FROM SOUTHEASTERN BRAZIL

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Running title: A new species of *Sybota* from Southeastern Brazil.

ABSTRACT. In this paper, we describe and illustrate a new species of *Sybota* based on specimens collected in the states of Rio de Janeiro and São Paulo, Southeastern Brazil.

Keywords: Araneae, Uloboridae, *Sybota*, systematics.

INTRODUCTION

The genus *Sybota* Simon, 1892 was defined by Opell (1979) as having the posterior lateral eyes on prominent tubercles and a posterior abdominal projection extending beyond the spinnerets. This first character is also present in the closely related genera *Orinomana* Strand, 1934 and *Miagrammopes* O.P.-Cambridge, 1869 (Coddington 1990). The abdominal projection, however, is shared only by *Polenecia* Lehtinen 1967, a monotypic genus with distribution restricted to the Mediterranean region, in Europe and Africa. These two genera differ in relation of the arrangement of the anterior eye row, recurved in *Sybota* and procurved in *Polenecia*. In addition, *Polenecia* lacks PLE tubercles.

Opell (1979) included three species in his revision, the Chilean *S. abdominalis* (Nicolet 1849) and *S. osornis* Opell 1979, and the Argentinean *S. mendozae* Opell 1979. Grismado (2001) redescribed the holotype of *S. rana* (Mello-Leitão 1941), from Salta Province, Argentina, and described a new species, *S. atlantica*, collected in the coast of Buenos Aires Province, also in this same country. He noted that the Argentinean species present comparatively smaller spermatheca, with longer and convoluted copulatory ducts. Besides they also differ from Chilean species by having a longer carapace with anterior median eyes on a tubercle and by the epigynum presenting a posterior notch. Both authors overlooked *S. zenzesi* (Mello-Leitão 1945), a species known only by one male collected in Puerto Victoria, Misiones Province, Argentina.

In this paper we describe the first Brazilian species of the genus *Sybota*. *S. demariai* n.sp. presents the abdominal projection and PLE on tubercles, but differ from both Chilean and Argentinean species in relation of the spermatheca and morphology of the ducts.

The specimens examined were deposited in the spider collection of the Instituto Butantan, São Paulo, Brasil (IBSP, curator A. D. Brescovit). Female epigynum were dissected, and examined and illustrated immersed in clove oil. All measurements are in millimeters.

RESULTS

Sybota demariai, n. sp.

(Figs. 1-9)

Types.- Female holotype from Volta Redonda, Área de Relevante Interesse Ecológico Floresta da Cicuta, 22°31'S 44°07'W, State of Rio de Janeiro, Brazil, 31.VIII.2002, M. O. Gonzaga col., deposited in IBSP. Female paratype from the same locality.

Male paratype from Itanhaém, Estação Ecológica da Juréia, Guarau - Núcleo Arpoador, State of São Paulo, Brazil, 16-20.III.1997, A.D. Brescovit *et al.* col., deposited in IBSP.

Etymology.- The specific name honors professor Mário De Maria, first scientific advisor of both authors.

Diagnosis.- Females and males differ from any other species of *Sybota* by having abdominal humps (Figs. 1-3). The female epyginum is extremely simple, with a ventral mound (Fig. 4) and a posterior plate with two small copulatory openings (Fig. 5). Copulatory and fertilization ducts are separated, unlike in any other *Sybota* females (Fig. 6). Males can be distinguished from *S. atlantica* by presenting a shorter embolus (Fig. 7), and from all other species by the median apophysis with four conspicuous distal projections (Fig. 7, 8). That sclerite presents a large flattened ventral projection, a concave prolateral one, a hyaline retrolateral and a median sclerotized and pointed (Fig. 9).

Description.- *Female (holotype).* Carapace yellow scattered with dark spots and covered with white hairs (Fig. 1). Cephalic region higher than thoracic (Fig. 2). Eyes on tubercles. Legs and sternum yellow, also with dark spots. Abdomen dorsally whitish with darker transversal bands. Venter dark around the epigynum, with a white mark between the spinnerets and the epigastric furrow. Dorsum of abdomen presenting two pairs of humps: an anterior pair smaller and pointed followed by another larger one (Figs. 1, 2). Abdomen with an extension beyond the spinnerets presenting many bristles. Tibia of all legs with a strong median or distal spatulated setae. Femur I, II and III with a row of long trichobotria. Epigynum lightly sclerotized, presenting a small median mound. Copulatory and fertilization ducts separated, both connecting directly with the spermatheca. Total length 3.6, carapace 1.2 long, 1.0 wide. First femur 1.6; patella and tibia 1.7; metatarsus 1.2; tarsus 0.6. Second femur 1.0; patella and tibia 0.9; metatarsus 0.7; tarsus 0.4. Third femur 0.9; patella and tibia 0.7; metatarsus 0.5; tarsus 0.4. Fourth femur 0.8; patella and tibia 1.1; metatarsus 0.6; tarsus 0.2.

Male. - Colors and spination as in females. Total length 2.2, carapace 0.9 long, 0.8 wide. First femur 1.5; patella and tibia 1.6; metatarsus 1.2; tarsus 0.6. Second femur 0.8; patella and tibia 0.7; metatarsus 0.5; tarsus 0.4. Third femur 0.5; patella and tibia 0.5; metatarsus 0.3; tarsus 0.2. Fourth femur 0.6; patella and tibia 0.8; metatarsus 0.5; tarsus 0.4.

Distribution.- Known only from Southeastern Brazil. This is the northernmost and easternmost records for the genus (Fig. 10).

Additional material examined.- BRASIL: *São Paulo*: Atibaia, Parque Florestal do Itapetinga, 23°10'S 46°25'W, X.2002, L.M. Rosseto & G. Machado col., 1♀ (IBSP).

ACKNOWLEDGEMENTS

We are especially grateful to Angela M.F. Pacheco for the illustrations, and Antonio D. Brescovit and Cristina A. Rheims (IBSP) for helpful suggestions on the manuscript. We are also indebted to Fundação CSN and IBAMA for allowing our studies in the ARIE Floresta da Cicuta. This study was financed by FAPESP doctoral fellowship grants (Proc. 99/06089-4 to M.O. Gonzaga and 99/05659-8 to A.J. Santos).

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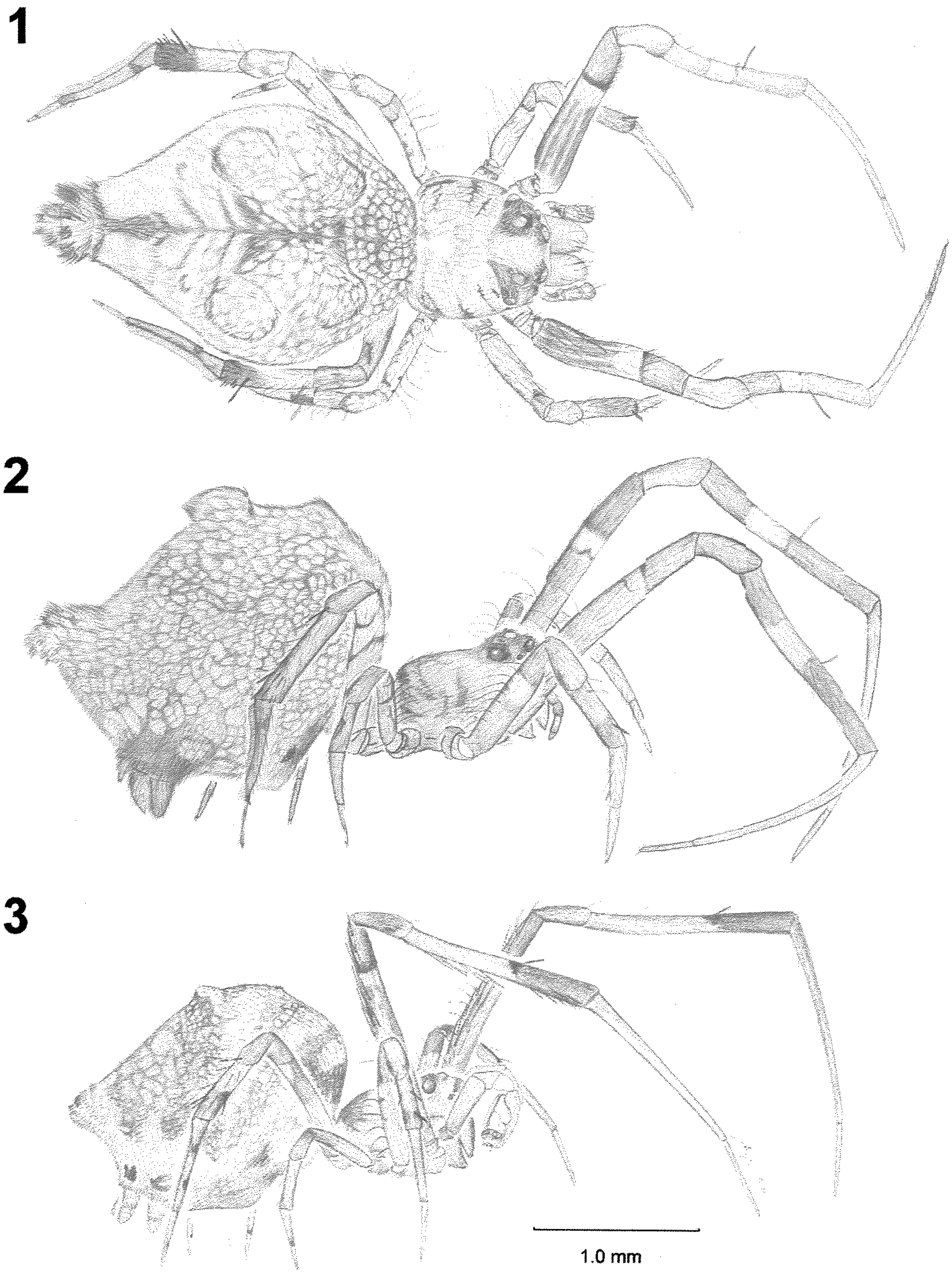
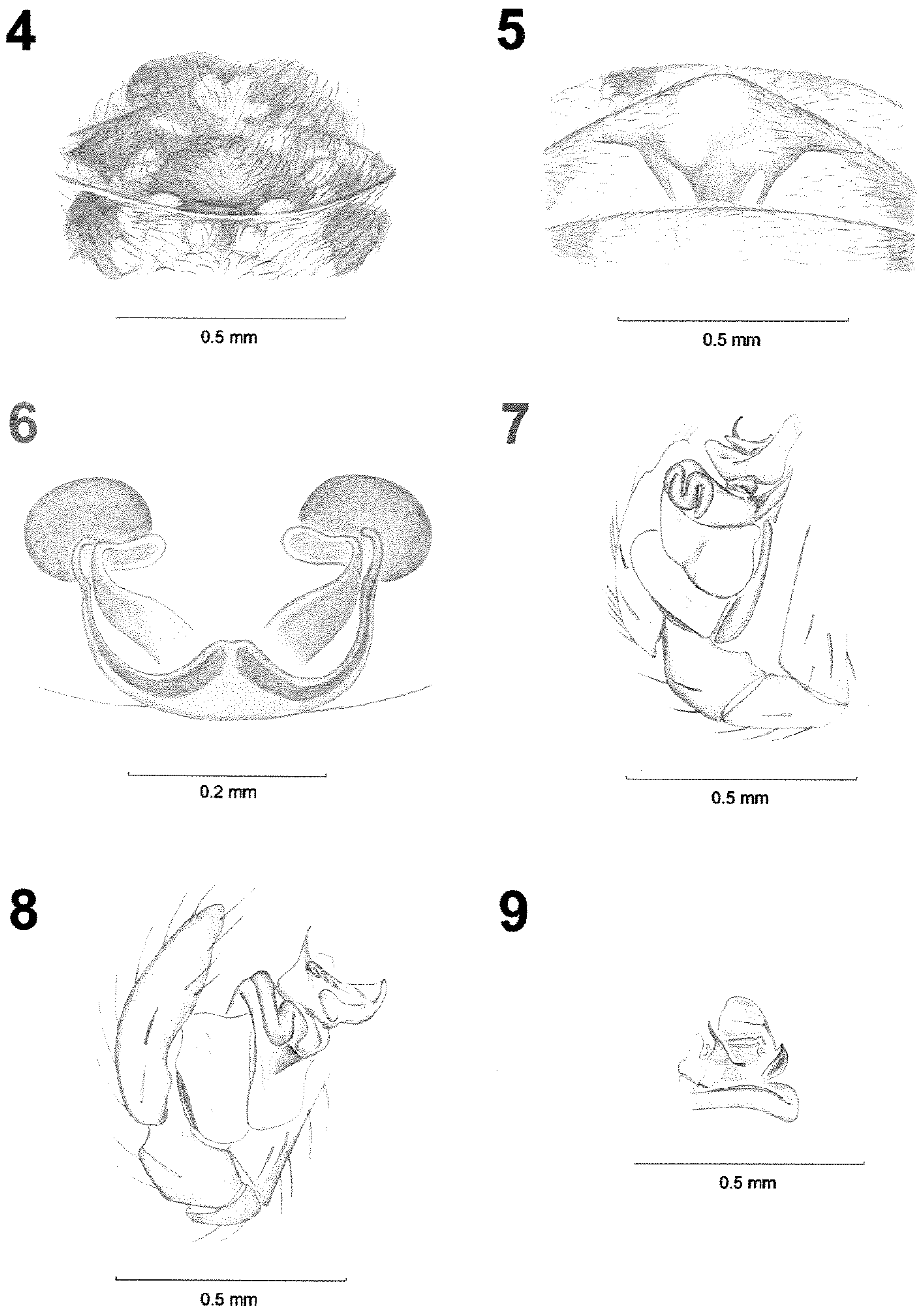


Figs. 1-3.- *Sybota demariai* new species. 1. Female, dorsal view; 2. Female lateral view; 3. Male lateral view.



Figs.4-9.- Genitalia of *Sybota demariai* new species. 4. Epigynum, ventral view; 5. Epigynum, posterior view; 6. Cleared epigynum, dorsal view; 7. Left male palp, ventral view; 8. Same, retrolateral; 9. Detail of the median apophysis, dorsal view.

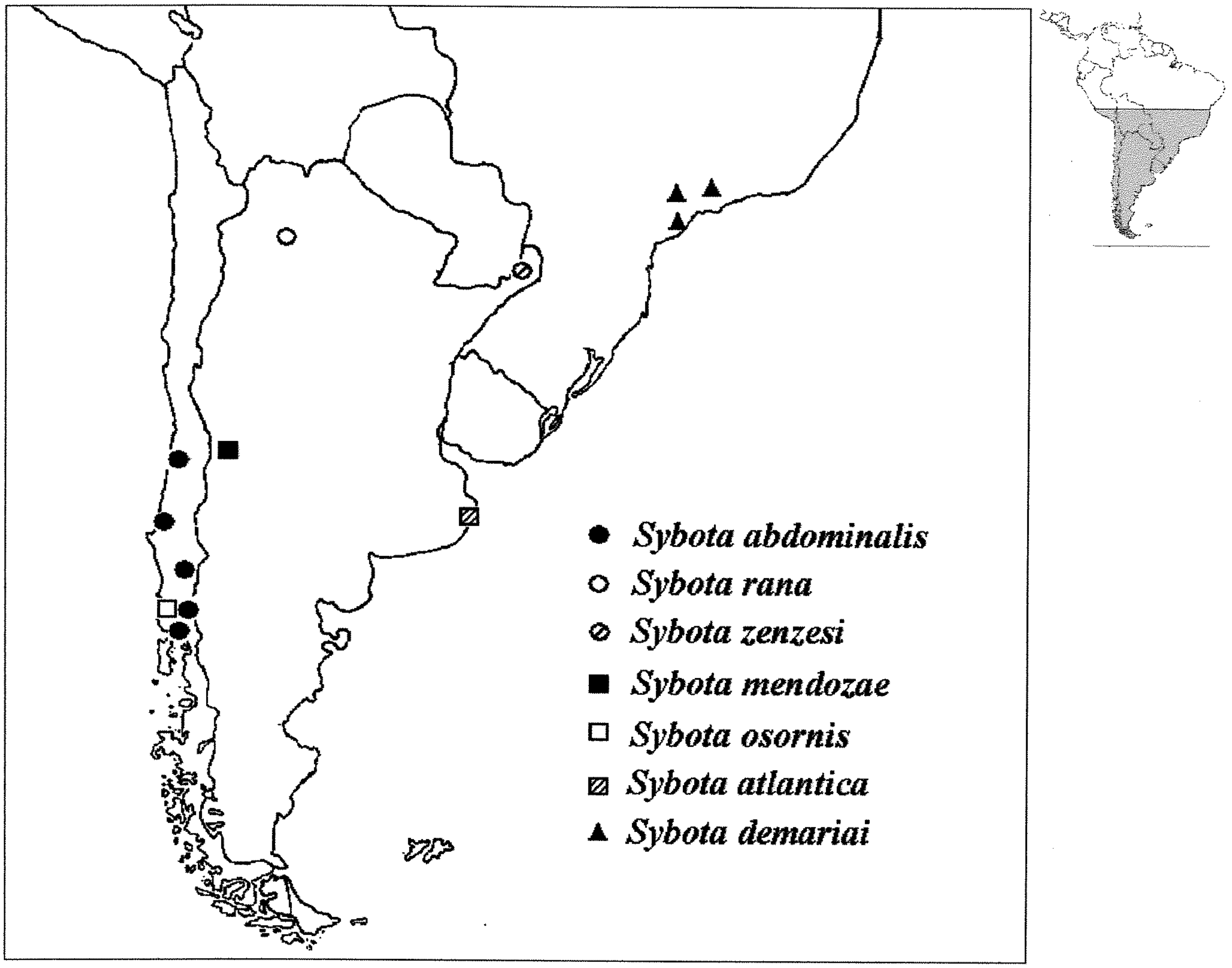
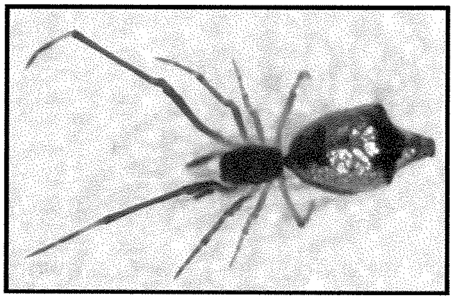


Fig. 10.- Geographic distribution of *Sybota* species.

Anexo 3

Synonymy of *Argyrodes rigidus* Exline & Levi 1962 with *Argyrodes striatus* Keyserling 1891 (Araneae: Theridiidae), with notes on foraging behaviour and host species selection



No prelo: Bulletin of British Arachnological Society

SYNONYMY OF *ARGYRODES RIGIDUS* EXLINE & LEVI 1962 WITH *ARGYRODES STRIATUS* KEYSERLING 1891 (ARANEAE: THERIDIIDAE), WITH NOTES ON FORAGING BEHAVIOUR AND HOST SPECIES SELECTION

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Running title: Synonymy of *Argyrodes rigidus* with *A. striatus.*

SUMMARY

Many species of the spider genus *Argyrodes* are known from a single sex. This is the case of two species from Cancellatus group previously collected in Southern and Southeastern Brazil: *A. rigidus*, known only from females, and *A. striatus*, from males. In this study I collected *Argyrodes* from webs of six host species in an area of Atlantic Forest in São Paulo State. A large number of females of *A. rigidus* and males of *A. striatus* were collected, sometimes in the same host web, suggesting that they are conspecifics. Therefore, I considered *A. rigidus* a junior synonymy of *A. striatus*. I observed these spiders feeding on a stored food bundle wrapped by the host and gleaning small diptera from the host web. *Verrucosa arenata* (Araneidae) was the main host species. The preference for this hosts may be a consequence of their relatively larger webs, tolerance to the presence of kleptoparasites and their behaviour of packing prey items, allowing the exploitation of large resource patches by *Argyrodes*.

Key-words: *Argyrodes*, kleptoparasitism, foraging behaviour, host species selection

INTRODUCTION

The worldwide distributed genus *Argyrodes* comprises 226 species, 32 of which known only by males, 63 by females and 3 by juveniles (Platnick, 2003). Members of this genus exhibit a diversified range of foraging strategies, including particular techniques of araneophagy and kleptoparasitism (Whitehouse *et al.*, 2002). Many species live in webs of other spiders, gleaning small insects, stealing and consuming web threads and stored food bundles, or even sharing food with the host, ingesting part of the pre-digested prey items. Some species attack the hosts when they are in the vulnerable period of molting. Others capture the hosts throwing lines of stick silk over them or simply grabbing small individuals with their front legs (see Eberhard, 1979; Smith Trail, 1980; Tso & Severinghaus, 1998; Whitehouse, 1997; Whitehouse *et al.*, 2002).

Exline & Levi (1962) revised the American species of *Argyrodes*, dividing the genus into six species groups. These groups were established on the basis of the morphology of cephalic region and clypeus of males, and shape of abdomen and genitalia. Behavioural observations to date suggest that spiders within four of the species groups use similar foraging strategies. Rhomphacea and Ariamnes groups capture spiders by throwing silk over them, species of the group Argyrodes seem to be specialized on kleptoparasitism, and the members of Trigonum group forage using both kleptoparasitism and araneophagy, attacking other spiders directly biting them. However, there is no information about the group Cordillera and the large group Cancellatus includes species with very distinct habits. This variation, in addition to the size of this last group and its morphological diversity, suggests that Cancellatus is not monophyletic (Whitehouse *et al.*, 2002) and emphasizes the need for additional behavioural data on more species of this group.

There are 55 American species of *Argyrodes* included in Cancellatus group. However, information about most of them is restricted to morphological descriptions and geographic distribution. Eleven species are known only by females and eight only by males (Exline & Levi, 1962; González & Carmen, 1996; Levi, 1967). At least part of this taxonomic problem could be easily solved with additional surveys near or at the areas where the type material was collected.

MATERIAL AND METHODS

I inspected all the webs of 11 species of potential hosts located along the forest borders of three trails in the Parque Estadual Intervales, a large area of Atlantic Forest (49,000 ha) located in Ribeirão Grande, State of São Paulo, Brazil (24°16'S; 48°25'W). The surveys were initially designed to evaluate the frequency of occupation of webs of *Cyclosa morretes* and *Cyclosa fililineata* (Araneidae) by kleptoparasites, and extended latter to other possible hosts in the area.

The inspections were performed during the day time (8:00 to 17:00) in May and June of 2003, corresponding to the dry season. The web owners and any other spiders present or with threads connected to host webs were captured, preserved in alcohol 70%, and identified in laboratory. The specimens examined were deposited in the spider collection of the Instituto Butantan, São Paulo.

The first 10 webs of each of the most abundant host species located in the main trail were measured (vertical and horizontal diameters), to compare the area available for colonization by kleptoparasites. Web area was calculated using the ellipse formula $(d_v/2)(d_h/2)\pi$ and compared by ANOVA and Tukey's HSD test. I also measured the carapace width of hosts and *Argyrodes* specimens collected in their webs to evaluate the relation between these spider's size.

RESULTS AND DISCUSSION

Distribution and taxonomy

I found 64 specimens of *Argyrodes* in webs of six host species (Tab. 1): 24 males of *A. striatus*, 31 females of *A. rigidus* and 9 specimens of a new species (1 male, 1 female and 7 juveniles), all of them belonging to Cancellatus group according to Exline & Levi (1962) definition. A total of 1130 webs of these hosts were examined during the survey. Five species of potential hosts did not present any kleptoparasites in their webs. I also found three other males of *A. striatus* and another female of *A. rigidus* in threads without connection with any other web, and two males of *A. striatus* and one female of *A. rigidus* co-occupying an abandoned host web. The absence of males of *A. rigidus* and females of *A. striatus* in Parque Estadual Intervales, in addition to the observation that both species occur in the same host webs, strongly suggests that they are conspecifics.

Exline & Levi (1962) described *A. rigidus* based on two females from Teresópolis, State of Rio de Janeiro, Brazil. They included an observation in the diagnosis of *A. rigidus* that this could be the female of *A. striatus*, but did not mentioned why they came to this conclusion. Males, but not females, of this last species were previously collected in some localities of South and Southeast Brazil, but not in the type locality of *A. rigidus* (Exline & Levi, 1962; Platnick, 2003). This is the first record of males and females collected in the same locality. Therefore I consider *Argyrodes rigidus* Exline & Levi 1962 a junior synonymy of *Argyrodes striatus* Keyserling 1891.

Behavioural observations

I observed one male of *A. striatus* feeding on a large wasp captured and entangled by *Verrucosa arenata* (Walckenaer 1842) (Fig. 1) and a female gleaning small diptera entangled in a web of another individual of this same host species. *A. striatus* were generally found at their own threads connected with the webs of their hosts, but I observed many individuals entering the sticky spiral region without attract the resident spider. The number of specimens of *A. striatus* per host web varied from 1 to 5 (mean = 1.33, sd = 0.84, n = 39 webs). Most hosts, with exception of some immature individuals of *Cyclosa fililineata*, are larger than the invaders (Tab.2) and probably are not susceptible to predation by them.

The relatively larger number of individuals in webs of *V. arenata* in relation to the other most abundant host species in Parque Estadual Intervales may be due to the higher web area available for occupation (Fig. 2) (ANOVA, $F_{4,45} = 36.3$, $p<0.001$). Besides, webs constructed by *Verrucosa* often intercept large prey items and the host behaviour of wrapping and fixing food bundles in the web allows the exploitation of profitable resource patches by the kleptoparasites. In addition, large hosts often neglect very small insects, which could be captured by *A. striatus*, and probably are less capable to locate and attack the small invaders. Henaut (2000) observed that *V. arenata* and, especially *Gasteracantha cancriformes* (Linnaeus 1785), rarely show aggressive behaviours towards *Argyrodes* *globosus* (Keyserling 1884). Other smaller hosts, such as *Leucauge argyra* (White 1841), were much more aggressive.

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Table 1: Total number of webs of potential hosts inspected during the surveys and occupied by *Argyrodes*.

Host	**Webs inspected**	**Webs only with *A. striatus* males**	**Webs only with *A. striatus* females**	**Webs with *A. striatus* males and females**	**Total number of *A. striatus* collected**	**Total number of the new sp. collected**
Araneidae						
Alpaida veniliae (Keyserling 1865)	26	0	0	0	0	0
Araneus vincibilis (Keyserling 1893)	1	0	0	1	3♂,2♀	0
Argiope argentata (Fabricius 1775)	6	0	0	0	0	0
Cyclosa fililineata Hingston 1932	637	2	0	0	3♂	2juv.
Cyclosa morretes Levi 1999	168	2	2	3	5♂,6♀	2juv.
Eustala sp.	28	0	0	0	0	0
Gasteracantha cancriformes (Linnaeus 1758)	4	0	0	0	0	0
Micrathena plana (C.L. Koch 1836)	3	0	0	0	0	0
Parawixia audax (Blackwall 1863)	11	0	1	0	1♀	0
Verrucosa arenata (Walckenaer 1842)	158	9	14	3	13♂,20♀	1♂, 3juv.
Tetragnathidae						
Leucauge sp.	155	0	2	0	2♀	1♀
Lycosidae						
Aglaoctenus lagotis (Holmberg 1876)	5	0	0	0	0	0
TOTAL	1202	13	19	7	24♂,31♀	1♂,1♀,7juv.

Table 2: Carapace width (mm) of hosts and kleptoparasites found in their webs.

Host species	**Host carapace width (mean ± sd) (n)**	***A. striatus* carapace width (mean ± sd) (n)**
Verrucosa arenata	2.46 ± 0.42 (26)	0.56 ± 0.07 (33)
Araneus vincibilis	3.8 (1)	0.55 ± 0.11 (5)
Leucauge sp.	0.77 ± 0.05 (2)	0.50 (1)
Cyclosa fililineata	0.62 ± 0.07 (2)	0.57 (1)
Cyclosa morretes	1.37 ± 0.09 (4)	0.54 ± 0.07 (10)
Parawixia audax	3.33 (1)	0.47 (1)

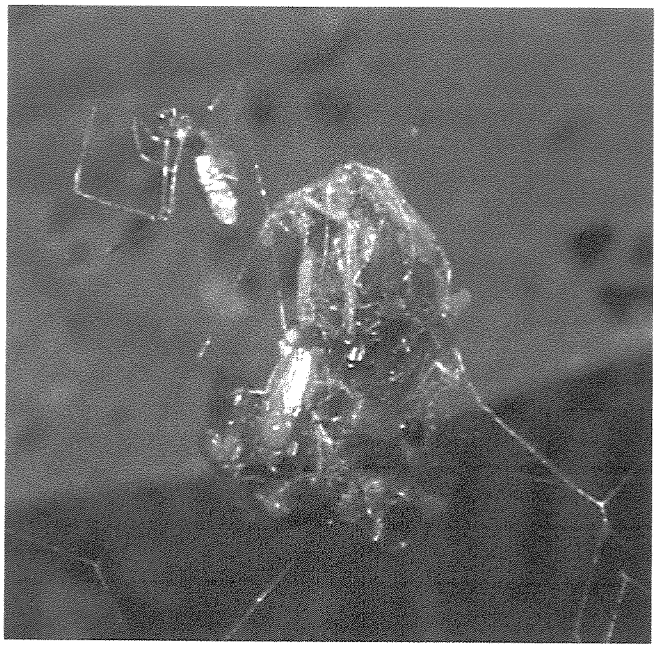


Fig.1: Male of *Argyrodes striatus* after feeding on a prey captured by *Verrucosa arenata*. This food bundle was also attacked by kleptoparasitic flies.

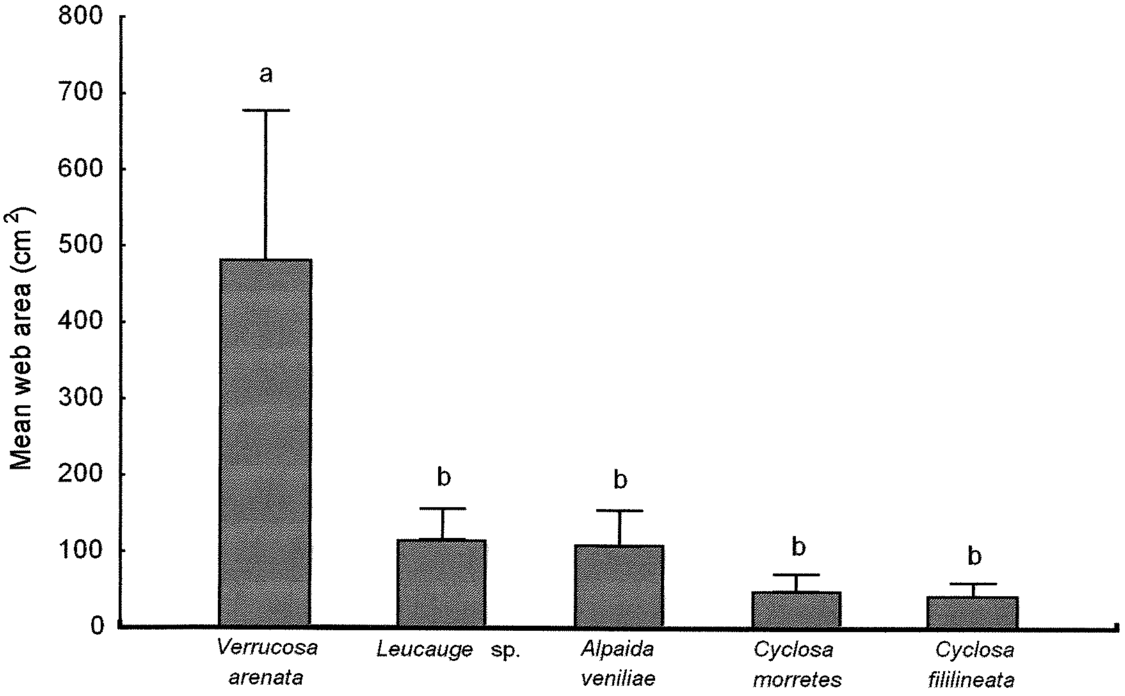
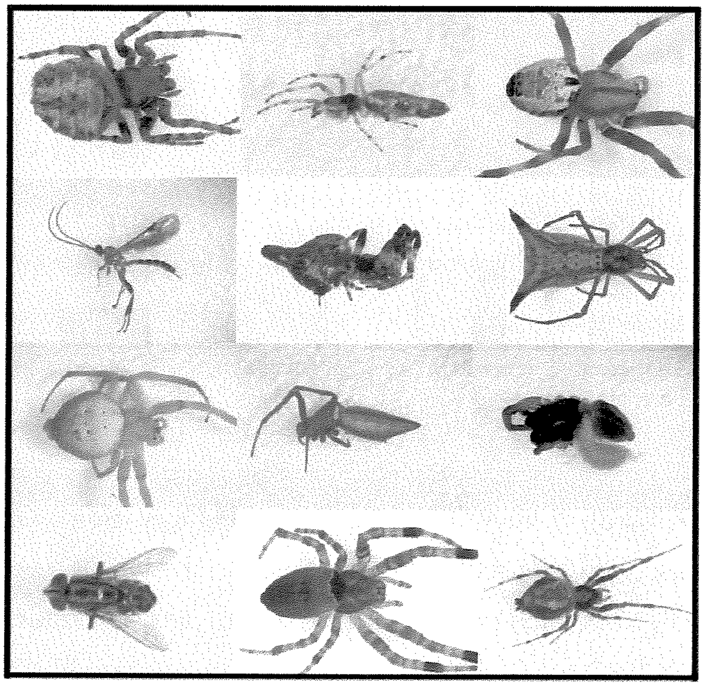


Fig. 2: Web area of the most abundant potential hosts for *A. striatus* in Parque Estadual Intervales (Mean ± sd, n=10 for all host species). Columns labelled with the same letter do not differ significantly from each other, while those with different letters differ at the 0.05 leve according to Tukey's HSD test.

Discussão



DISCUSSÃO GERAL

Uma análise da literatura disponível sobre predadores e parasitas de aranhas evidencia algumas deficiências importantes no conhecimento atual sobre interações envolvendo estes organismos. O primeiro problema é a escassez de trabalhos sobre alguns grupos taxonômicos, como os himenópteros parasitóides da família Scelionidae (e.g. *Baeus, Ceratobaeus, Idris*). Muito pouco é conhecido sobre seus hábitos e sobre o impacto de sua ocorrência sobre populações de hospedeiros. Além disso, não existem estudos taxonômicos que permitam a identificação de grande parte das espécies descritas (que provavelmente representam ainda uma porção muito pequena da diversidade real do grupo). A situação dos endoparasitas de ovos do gênero *Baeus* é típica. Existem atualmente 24 espécies descritas distribuídas por todo o mundo (apenas seis na região neotropical, onde o último trabalho sobre o gênero foi publicado há mais de 30 anos - Loiacono 1973) (N. Stevens, com. pessoal). Stevens & Austin (em prep.), durante coletas recentes na Austrália, encontraram 17 novas espécies, quase dobrando o número de espécies conhecidas e multiplicando por seis o número de espécies australianas.

Mesmo em grupos relativamente bem estudados, como vespas caçadoras das famílias Sphecidae e Pompilidae, existe uma grande carência de dados sobre espécies que ocorrem em regiões tropicais e equatoriais. O gênero *Trypoxylon* (Sphecidae) constitui um bom exemplo da distribuição geográfica desigual das pesquisas. Embora constitua um grupo cosmopolita e muito diversificado, com mais de 500 espécies descritas (Coville 1987), existem dados sobre provisionamento de ninhos para apenas cerca de 40 delas (Blacklegde *et al.* 2003). Grande parte dos trabalhos sobre essas espécies foram realizados nos Estados Unidos ou Inglaterra. Entre aqueles desenvolvidos em áreas tropicais, a maioria foi feita com espécies da Costa Rica. Praticamente nada é conhecido sobre as espécies africanas, asiáticas e, na América do Sul, os trabalhos publicados que incluem dados sobre a utilização de aranhas restringem-se a três espécies (*T. lactitarse*, *T. antropovi* e *T. rogenhoferi*) (veja Blackledge *et al.* 2003, Gonzaga & Vasconcellos-Neto, em prep.).

Trypoxylon albonigrum foi a quarta espécie do gênero estudada no Brasil em relação ao provisionamento dos ninhos. Assim como as demais (veja Camillo 1999, Camillo & Brescovit 1999a, b, Gonzaga & Vasconcellos-Neto em prep.), esta espécie capturou preferencialmente poucos tipos de presas para alimentar suas larvas. De acordo com Coville (1987), o principal fator determinante da seleção de presas por Sphecidae seria a abundância relativa de cada espécie de aranha nas áreas utilizadas para caça. Além disso, haveria uma limitação máxima de tamanho de presa relacionada à capacidade de transporte e imobilização, e mínima, relacionada aos custos de transporte de um grande número de itens para provisionar cada célula do ninho. Apenas estas duas variáveis, entretanto, não explicam a seleção de presas armazenadas nos ninhos de *T. albonigrum* (e também de *T. larctitarse*, outra espécie coletada durante este estudo). Aranhas dos gêneros *Eustala*, *Parawixia* e *Araneus* foram capturadas com freqüências muito maiores que as esperadas com base na estimativa de suas abundâncias relativas no campo. Por outro lado, os gêneros de aranhas orbitelas coletados em maior abundância durante as amostragens para determinação da disponibilidade de presas no P.E. Intervales (*Cyclosa*, *Leucauge* e *Verrucosa*) não foram capturados pelas vespas. Apesar da maior parte dos indivíduos desses gêneros coletados pelos pesquisadores apresentar tamanho corporal menor que o das presas comumente capturadas, adultos de *Cyclosa* e *Leucauge*, e mesmo alguns imaturos de *Verrucosa*, apresentaram tamanhos similares ao dos indivíduos de *Eustala* encontrados nos ninhos.

Embora parte das diferenças entre as amostragens realizadas pelos pesquisadores e pelas vespas certamente deva-se a diferenças na percepção de sinais visuais indicadores da presença de aranhas (teias, abrigos, estabilimentos) ou das próprias aranhas (coloração, contraste com o fundo), os resultados obtidos neste estudo sugerem que nem todas as aranhas com tamanho semelhante são igualmente susceptíveis ao ataque por vespas. O tipo de teia e estruturas de defesa, por exemplo, constituem aspectos que devem ser considerados na análise de seleção de presas. Blacklegde *et al.* (2003) apresentam dados que corroboram a hipótese de que teias tridimensionais conferem maior proteção contra o ataque por vespas que as teias orbiculares, bidimensionais. Nossos resultados sugerem que, entre aranhas construtoras de teias orbiculares, outras características das teias podem ser importantes para defesa. Três das espécies mais comumente coletadas durante as amostragens para determinação da disponibilidade de presas e ausentes nos ninhos de vespas (*Cyclosa morretes*, *C. fililineata* e *Verrucosa arenata*), por exemplo, constroem estabilimentos. Estas estruturas podem constituir elementos de distração durante a captura (veja Blackledge & Wenzel 2001) ou reduzir a probabilidade das aranhas serem localizadas (veja Eberhard 1973).

A análise das teias construídas por diferentes populações de *C. morretes* e *Cyclosa fililineata* mostrou que, ao contrário do que ocorre com aranhas do gênero *Argiope* (Araneidae), não existe uma grande variação na freqüência de construção de estabilimentos. Seah & Li (2002) demonstraram experimentalmente que fêmeas adultas de *Argiope versicolor* são mais propensas a adicionar estabilimentos às suas teias quando estão bem alimentadas. O mesmo padrão foi observado por Blackledge (1998) para *A. aurantia* e *A. trifasciata*, que além da freqüência de construção, alteram também o tamanho de seus estabilimentos de acordo com sua alimentação. De acordo com Seah & Li (2002), as condições nutricionais das aranhas determinariam a quantidade de energia que pode ser investida na construção de estruturas de defesa. Assim, aranhas que passaram muito tempo sem alimento tenderiam a utilizar suas reservas protéicas na construção de teias de captura e não de adornos para defesa. Em *Cyclosa*, a substituição dos estabilimentos de seda por estruturas similares compostas por detritos pode minimizar os gastos energéticos, possibilitando que todas as aranhas (mesmo aquelas em estado de carência nutricional) utilizem esta estratégia defensiva.

Todas as populações apresentaram os mesmos tipos de estruturas de seda e detritos. Variações ontogenéticas restringiram-se a diferentes freqüências de estabilimentos com detritos dispostos de forma linear contínua e descontínua em *C. morretes*. Estruturas descontínuas são mais comuns em indivíduos imaturos, possivelmente porque ainda não acumularam detritos suficientes para a construção de colunas completas. Apesar da relativa homogeneidade na forma dos estabilimentos, a posição ocupada pelas aranhas em meio aos detritos é muito variável. Essa imprevisibilidade na localização das aranhas pode ser importante para dificultar o ataque por vespas parasitóides. Ataques em posições erradas permitiriam que a aranha tivesse tempo suficiente para saltar da teia ou correr para sua periferia, abrigando-se na vegetação.

Herbestein *et al.* (2002) sugerem que os estabilimentos de detritos deveriam ser considerados como um fenômeno comportamental distinto dos estabilimentos de teia. Os dados referentes ao processo de reconstrução dessas estruturas após sua remoção, entretanto, mostram que as duas espécies de *Cyclosa* estudadas adicionam estabilimentos de seda às suas teias quando detritos não estão disponíveis. O mesmo padrão comportamental foi descrito para *Allocyclosa bifurca* (Araneidae) (Eberhard 2003). Isto indica que os estabilimentos de seda podem apresentar a mesma função das estruturas contendo detritos, embora estas últimas sejam preferencialmente construídas sempre que possível.

Allocyclosa bifurca, espécie inicialmente incluída no gênero *Cyclosa* e transferida por Levi (1999), apresenta ainda uma série de características interessantes que possivelmente estão associadas à construção de seus estabilimentos. A primeira delas é uma mudança na coloração das aranhas durante sua maturação. Indivíduos jovens apresentam coloração marrom, similar à coloração dos detritos presentes em seus estabilimentos. Já as fêmeas adultas apresentam coloração esverdeada, muito parecida com o padrão dos estabilimentos de seda que contém as ootecas. Além disso, este último tipo de estabilimento contém tufos de seda que assemelham-se às protuberâncias existentes nos abdomens das aranhas. Assim como *C. morretes* e *C. fililineata*, *A. bifurca* permanece exposta no centro de sua teia durante o dia, em posição críptica (com as pernas junto ao corpo) entre segmentos de seda/ootecas ou detritos. Estas características também indicam que os estabilimentos apresentam função de proteção, possivelmente dificultando a localização da aranha por seus predadores.

Os testes de atração de presa realizados com estabilimentos de *Cyclosa morretes* e *C. fililineata* confirmaram a ineficiência destas estruturas para aumentar a freqüência de interceptação de insetos pelas teias. Como a hipótese de atração de presas está baseada nas propriedades reflexivas das teias (Craig & Bernard 1990), era esperado que estabilimentos contendo detritos não fossem capazes de desempenhar essa função. Já os testes com modelos artificiais em forma de aranhas e estabilimentos apresentaram resultados que corroboram a hipótese de defesa. Modelos em forma de aranha foram muito mais atacados. É provável que predadores com imagem de busca com a forma do corpo de uma aranha não associem uma forma linear com a presença de suas presas. A baixa freqüência de ataque sobre os modelos com duas cores contrastantes (segmentos brancos simulando estabilimentos de seda e escuros com forma similar ao corpo de uma aranha) confirma que mesmo as colunas de seda adicionadas quando os detritos não estão disponíveis poderiam minimizar o risco das aranhas serem localizadas.

Apesar de ignoradas por vespas-caçadoras, *C. fililineata* e *C. morretes* foram atacadas por ichneumonídeos e scelionídeos parasitóides durante nossos estudos. A freqüência de ataque por *Polysphincta* sp. (Ichneumonidae), no entanto, foi baixa para as duas espécies. Indivíduos portando larvas de tamanhos reduzidos constroem teias normais, mas aqueles encontrados com larvas grandes apresentavam teias muito alteradas. A alteração das teias, com diminuição do número de raios e ausência de espiras, pode representar um tipo de manipulação do hospedeiro para diminuir a conspicuidade e o risco de destruição da estrutura que abrigará o casulo do parasitóide. Teias completas ofereceriam maior risco de interceptação de insetos, o que poderia romper fios essenciais para a sustentação do casulo. A manipulação de hospedeiros já foi descrita para outro parasitóide de aranhas da mesma subfamília de *Polysphincta*, Pimplinae. Neste caso, descrito por Eberhard (2000a, 2000b, 2001), as teias construídas por *Plesiometa argyra* (Tetragnathidae) também permanecem inalteradas até que a larva de *Hymenoepimecis argyraphaga* esteja bem desenvolvida. O tipo de teia construído na noite em que a larva constrói seu casulo, entretanto, é muito modificado, garantindo um suporte mais resistente que a teia original. A comparação entre teias construídas por *C. fililineata* com parasitóides de diversos tamanhos sugere que *Polysphincta* sp. não induz uma mudança comportamental tão súbita. Alterações graduais poderiam também ser conseqüência do processo de debilitação física sofrido pelas aranhas durante o crescimento das larvas, e não devido à indução de comportamentos específicos através da inoculação de compostos produzidos pelas larvas. A confirmação da hipótese de manipulação depende ainda de estudos adicionais envolvendo o acompanhamento do desenvolvimento das larvas e registro do comportamento dos hospedeiros.

Embora o ataque por *Polysphincta* tenha sido pouco freqüente, parasitóides de ovos do gênero *Baeus* atacaram uma grande proporção das ootecas de *C. morretes* observadas. A maior incidência desses parasitóides em ootecas de *C. morretes* pode ser um reflexo da maior disponibilidade de ovos em estabilimentos desta espécie e do maior volume médio dos ovos, o que proporciona uma maior quantidade de nutrientes para cada larva do parasitóide. É importante determinar, entretanto, como *Baeus* sp. localiza seus hospedeiros e se ootecas de *C. fililineata* são rejeitadas. Austin (1984) observou que, embora várias espécies de *Ceratobaeus* utilizem diferentes hospedeiros, todas elas ocorrem preferencialmente em apenas uma espécie. As espécies australianas estudadas por Austin são capazes de localizar as ootecas de seus hospedeiros (especialmente aranhas do gênero *Clubiona*, Clubionidae) apenas quando estas estão depositadas sobre as cascas de uma espécie de eucalipto. A localização de insetos fitófagos hospedeiros por muitos himenópteros parasitóides depende de sinais químicos. Os parasitóides podem guiar-se por substâncias presentes no próprio corpo do hospedeiro e/ou nas plantas utilizadas por eles (Vinson 1976), como ocorre com *Ceratobaeus*. É possível que *Baeus* sp. também utilize sinais químicos específicos para localizar seus hospedeiros, mas não existem estudos analisando estratégias de procura neste grupo.

Parte da diferença entre a abundância das duas espécies de *Cyclosa* no Parque Estadual de Intervales (*C. fililineata* foi muito mais abundante em todos os períodos de amostragem) pode ser um reflexo das diferenças nas taxas de mortalidade de ovos devido ao ataque por *Baeus*. Analisando apenas o número de ootecas e tamanho de ninhada das duas espécies, seria esperada uma maior abundância de *C. morretes*. É provável, entretanto, que muitos outros fatores estejam envolvidos na determinação da densidade populacional das duas espécies. É possível, por exemplo, que os indivíduos imaturos de *C. morretes* que constroem estabilimentos descontínuos sofram maior predação. Outra possibilidade é que as duas espécies estejam segregadas espacialmente e que a maior densidade de *C. fililineata* observada neste estudo restrinja-se ao local e/ou estrato amostrados.

Em muitos aspectos os dados obtidos nesta tese constituem apenas o início de linhas de pesquisa que devem ser estendidas. Esperamos que constituam um incentivo a novos trabalhos que nos permitam avançar um pouco mais em relação ao conhecimento sobre predadores e parasitas de aranhas e, especialmente, sobre as funções dos diversos tipos de estabilimentos construídos por aranhas orbitelas.

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