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Andréa Lúcia Teixeira de Souza

INFLUÊNCIA DA ARQUITETURA DE RAMOS VEGETATIVOS E INFLORESCÊNCIAS NA DISTRIBUIÇÃO DE ARANHAS EM PLANTAS

Orientador: Prof. Dr. João Vasconcellos-Neto
Co-orientador: Prof. Dr. Rogério Parentoni Martins

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BANCA EXAMINADORA

TITULARES:

Prof. Dr. João Vasconcellos Neto (orientador) ____________________

Prof. Dr. Thomas Michael Lewinsohn ____________________

Prof. Dr. Arício Xavier Linhares ____________________

Profa. Dra. Cláudia Maria Jacobi ____________________

Prof. Dr. José Eugênio Cortes Figueira ____________________

SUPLENTES:

Prof. Dr. Flávio Antônio Mäes dos Santos ____________________

Prof. Dr. Antônio Domingos Brescovit ____________________

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RESUMO

A arquitetura de ramos constitui um dos principais fatores que podem influenciar a diversidade e a abundância de aranhas que habitam plantas. Neste estudo, a abundância de aranhas foi comparada entre sete espécies de plantas arbustivas abundantes numa área de cerrado na Reserva Ecológica do Panga à 40km de Uberlândia, Minas Gerais. A número médio de aranhas por ramo foi positivamente relacionada com a complexidade estrutural dos ramos, descrita como número de folhas por unidade de volume do ramo. A composição de famílias e a distribuição do tamanho corporal de aranhas foram comparadas entre os ramos vegetativos de Baccharis dracunculifolia, Diplusodon virgatus e Bidens gardneri que possuiam diferentes níveis de complexidade estrutural. A distribuição do tamanho corporal foi similar entre as três espécies de plantas, no entanto a frequência relativa das famílias de aranhas diferiu entre elas. Oxyopidae e Salticidae ocorreram com mais frequência em B. dracunculifolia e Anyphaenidae foi a família mais abundante nas outras duas espécies que possuiam uma menor número de folhas por unidade de volume do ramo.

A abundância de aranhas foi comparada entre inflorescências e ramos vegetativos de quatro espécies de plantas: Microlicia helvola, B. dracunculifolia, D. virgatus e B. gardneri. O estado fenológico das plantas influenciou a abundância total e distribuição de famílias de aranhas, sendo que um maior número de aranhas foi registrado em inflorescências naturais e artificiais. Membros das famílias Anyphaenidae, Salticidae e Thomisidae ocorreram preferencialmente em inflorescências naturais quando comparadas aos ramos vegetativos. Inflorescências artificiais dispostas em Baccharis dracunculifolia

(Asteraceae) foram colonizadas por diferentes famílias de aranhas ao longo do ano. As inflorescências como habitat favorável para estes predadores é discutido em termos da disponibilidade de presas e refúgios e predação interespecífica. A distribuição de tamanhos de aranhas diferiu entre o tratamento e o controle. Aranhas maiores foram mais frequentes em inflorescências artificiais do que em ramos vegetativos. Além disto, a distribuição de tamanhos foi dependente de densidade em inflorescências, mas não em ramos vegetativos. Aranhas maiores ocorreram preferencialmente em inflorescências com baixa densidade, o que corrobora a hipótese de que aranhas devem estabelecer territórios apenas em microhabitats favoráveis.

A abundância de aranhas foi comparada entre inflorescências de 14 espécies de plantas. O número de flores abertas e o tamanho da flor foram os principais fatores na determinação da abundância total de aranhas em inflorescências, enquanto variáveis como complexidade estrutural e tamanho contribuíram para explicar a frequência das diferentes famílias nas inflorescências naturais. Os salticídeos foram mais abundantes em inflorescências com maior número total de flores, enquanto membros das famílias Anyphaenidae, Clubionidae e Oxyopidae foram mais comuns em inflorescências maiores e com o maior número de flores abertas. A abundância de tomisídeos foi correlacionada com o tamanho das flores. O efeito da cor, analisado separadamente através de experimentos usando inflorescências artificiais em _B. dracunculifolia_, foi significativo na determinação da abundância das famílias Anyphaenidae e Thomisidae, enquanto a forma da inflorescência (umbela vs. espiga) contribuiu para explicar a distribuição de Anyphaenidae e Clubionidae. O tamanho da flor, expresso através de seu diâmetro, influenciou a distribuição de tamanho de aranhas presentes em inflorescências naturais e

artificiais; aranhas de maior porte ocorreram com mais frequência em inflorescências compostas de flores de maior diâmetro.

Este estudo mostrou que diferenças na estrutura de inflorescências podem determinar a composição em famílias de aranhas que visitam flores, o que poderia influenciar indiretamente a dinâmica de populações de plantas através do impacto causado na comunidade dos insetos fitófagos.

ABSTRACT

Branch structural complexity is one of the main factors that influence the abundance and diversity of plant-dwelling spiders. In this study, spider abundance on seven abundant shrubby plant species was compared in a cerrado area at Reserva Ecológica do Panga, 40km south Uberlândia, Minas Gerais. Mean number of spiders per branch was positively correlated with the structural complexity of vegetative branches, described as the number of leaves per branch volume unit. Family composition and body size distribution of the spiders on vegetative branches were compared among Baccharis dracunculifolia, Diplusodon virgatus and Bidens gardneri, plant species with distinct structural complexity levels. Although a similar body size distribution was observed among the three plant species, the relative frequency of spider families was different. Oxyopidae and Salticidae occured more frequently on B. dracunculifolia, and Anyphaenidae was the most abundant on the other two species, which had a smaller number of leaves per branch volume unit.

Spider abundance on inflorescences vs vegetative branches was compared in four plant species: Microlicia helvola, B. dracunculifolia, D. virgatus and B. gardneri. The plant phenological state influenced both total abundance and composition of spider families, as spiders were more abundant on natural and artificial inflorescences. Members of the families Anyphaenidae, Saliticidae, and Thomisidae occurred preferentially on natural inflorescences relative to vegetative branches. Artificial inflorescences placed on Baccharis dracunculifolia (Asteraceae) were colonized by distinct spider families during one year. The favourable habitat constituted by inflorescences for those predators is

discussed in relation to prey and refuge availability, and interspecific predation. Spider size distribution differed between treatment and control branches, as larger spiders occurred more frequently on artificial inflorescences than on vegetative branches. The size distribution was density-dependent on inflorescences, but not on vegetative branches. Larger spiders occurred mainly on inflorescences with low densities, suggesting that an interaction between habitat features and density is plausible.

Spider abundance was also compared among inflorescences of 14 plant species. The number of open flowers and flower size were the main factors determining total spider abundance, and variables such as inflorescence structural complexity and size influenced the frequency of families on natural inflorescences. Salticids were more abundant on inflorescences with more flowers, while spiders of the families Anyphaenidae, Clubionidae, and Oxyopidae were more common on larger inflorescences with more open flowers. Thomisid abundance was positively correlated with flower size. When colour effects were analysed separately with an experiment using artificial inflorescences placed on B. dracunculifolia, there was a significant effect on the abundance of anyphaenids and thomisids, while inflorescence shape (umbel vs spike) influenced the distribution of anyphaenids and clubionids. Flower size (=diameter) influenced the size distribution of spiders both on natural and artificial inflorescences; larger spiders occurred more frequently on inflorescences with larger flowers. This study showed that differences on inflorescence structure may determine the composition of spider families which visit natural inflorescences, and this may indirectly influence the population dynamics of the plants used, through an impact on assemblages of phytophagous insects.

CAPÍTULO 1

ASPECTOS ECOLÓGICOS DE ARANHAS QUE HABITAM PLANTAS

ARANHAS COMO PREDADORES GENERALISTAS

A disponibilidade de presas está positivamente correlacionada à sobrevivência e ao sucesso reprodutivo em aranhas (Turnbull 1973, Wise 1979, Uetz 1992), uma vez que as taxas de aquisição do alimento podem influenciar seu crescimento e o número de ovos produzidos (Vollrath 1987, Morse 1988, Figueira e Vasconcellos-Neto 1992). Por outro lado, a predação parece constituir um dos principais fatores de mortalidade de aranhas (Waldorf 1976, Askenmo et al. 1977, Polis et al.1989, Gunnarsson 1996). Portanto, as decisões acerca da escolha de locais de forrageamento e do abandono de locais sub-ótimos devem influenciar a dinâmica populacional destes animais e devem estar condicionadas a um balanço entre a disponibilidade de presas e o risco de predação (veja Caraco e Gillespie 1986, Provencher e Vickery 1988, Kareiva et al. 1989).

Aranhas podem ser separadas em diferentes guildas conforme a definição de Root (1967) baseado nas similaridades morfológicas e de comportamento de captura de presas que podem refletir os tipos e tamanhos de presas consumidas. Assim, esta classificação pode ser baseada nas características taxonômicas a nível de família (Hatley e MacMahon 1980, Nentwig 1987, Ehmann e MacMahon 1996). Vários autores definirem guildas em aranhas agrupando diferentes famílias (p.ex. Hatley e MacMahon 1980, Robinson 1981, Scheidler 1990, Ehmann e MacMahon 1996), a divisão por famílias deve constituir a menor unidade que define as guildas uma vez que as diferenças na morfologia e táticas de captura são geralmente maiores entre famílias de aranhas do que entre membros da mesma família (veja a descrição abaixo) (Foelix 1996).

Os estudos sobre a distribuição de aranhas separadas em guildas ao invés de espécies tem a vantagem de poderem ser comparados com outros estudos feitos em diferentes regiões. Além disto, a separação de aranhas em guildas permite a inclusão de imaturos nos testes de hipóteses realizados em comunidades naturais (veja Turnbull 1973, Scheidler 1990, Ehmann e MacMahon 1996). Os indivíduos imaturos compõem a grande maioria do total de aranhas registradas, e normalmente são de difícil identificação a nível de espécie ou gênero.

Neste estudo as famílias de aranhas não-construtoras de teia mais abundantes foram Oxyopidae, Salticidae, Miturgidae, Anyphaenidae e Thomisidae e entre as construtores de teia, as mais abundantes foram as Araneidae, Theridiidae e Dictynidae. As aranhas não-construtoras de teia foram analisadas por família. No entanto, devido à baixa abundância relativa das aranhas construtoras de teia e às semelhanças entre elas com relação ao uso de armadilhas feitas de fios de seda, estas foram agrupadas num único grupo. Abaixo seguem as principais características morfológicas e comportamentais das famílias de aranhas não construtoras de teia baseadas em Comstock (1971), Nyffeler e Sterling (1994), Brescovit (1996), e Foelix (1996).

OXYOPIDAE – É composta por um grupo de espécies que possui grande agilidade sobre a vegetação herbácea, e folhas e ramos de árvores e arbustos. Como os Salticidae, estas aranhas podem, as vezes, saltar para capturar presas. Sua dieta é ampla podendo ser composta de até 10% de outras aranhas. Possuem hábitos diurnos e uma boa acuidade visual quando comparada a outros grupos de aranhas. Seus corpos são alongados e suas pernas delgadas e longas.

SALTICIDAE — São aranhas de médio e pequeno porte, corpo curto e pernas robustas, em especial os dois primeiros pares. De hábitos diurnos e uma boa acuidade visual, possuem olhos grandes e na vertical, com capacidade de visão binocular e formação de imagens a distâncias de até 10cm. Forrageiam na vegetação e frequentemente se utilizam de saltos para capturar presas, podendo até mesmo capturar insetos em vôo. Sua dieta é diversificada e outras aranhas podem compor até 20% de suas presas.

MITURGIDAE — Aranhas de médio porte, corpo e pernas alongadas e delgadas. São ativas à noite e passam o dia em abrigos achatados e tubulares feitos de fios de seda em folhas enroladas ou curvas. Possuem visão de curto alcance e são normalmente ineficientes na captura de insetos alados.

ANYPHAENIDAE – Aranhas de pequeno e médio porte e de hábitos noturnos possuem a aparência semelhante aos Miturgidae. Possuem o sistema traqueal muito desenvolvido, o que lhes permite deslocar-se com incrível rapidez em situações de perigo e captura de presas entre folhagens de plantas. Podem ser encontradas em florestas pluviais e zonas desérticas e semi-áridas, mas a sua distribuição e hábitos comportamentais são ainda desconhecidos.

THOMISIDAE — Possuem corpos curtos e largos e os dois primeiros pares de pernas são robustos e laterígrados, e que são utilizados para capturar presas. Seus olhos pequenos podem produzir imagens apenas a curta distância. Ao contrário das famílias anteriores, estas aranhas utilizam de estratégia do tipo tocaia, permanecendo paradas em escoderijos à espera de presas que se aproximem o suficiente para serem capturadas pelos dois primeiros pares de pernas. Em flores, podem capturar insetos como Lepidoptera, Hymenoptera e Diptera.

DISTRIBUIÇÃO DE ARANHAS EM PLANTAS

Plantas de espécies distintas abrigam diferentes densidades e estrutura de guildas de aranhas e estas diferenças podem ser devidas especialmente às variáveis relacionadas com a arquitetura destes habitats (Hatley e MacMahon 1980, Robinson 1981, Scheidler 1990, Gunnarsson 1990, Hurd e Fagan 1992, Mason 1992, Evans 1997, Halaj et al. 1997). As plantas são utilizadas por aranhas como substrato e variáveis como a complexidade estrutural de ramos ou o tamanho e forma das folhas devem estar relacionadas com abundância de presas e a disponibilidade de locais usados como refúgio e reprodução.

Algumas partes da planta dentro de uma mesma espécie são mais atrativas para insetos do que outras. Diferenças na exposição de luz e sombra, ou a presença de componentes nutritivos como nas folhas jovens, nectar e pólen podem levar a um mosaico relativamente complexo de sítios favoráveis para os insetos (veja Bernays e Chapman 1994) e consequentemente, esta segregação espacial deve influenciar a distribuição de predadores. A abundância de presas potenciais para aranhas é supostamente alta em flores, uma vez que são utilizadas como fonte de alimento por muitos insetos polinizadores e outros herbívoros (Louda 1982, Morse e Fritz 1982). Alternativamente, as aranhas podem também utilizar as estruturas florais como refúgio contra predadores e condições meteorológicas extremas, camuflagem, encontro de parceiros sexuais e locais de reprodução (Nentwig 1993, Johnson 1995). No entanto, poucos estudos consideraram o uso de flores por aranhas e os mecanismos envolvidos na decisão de escolha destes locais. Greco e Kevan (1994) discutiram a possibilidade das aranhas terem desenvolvido uma capacidade de escolha mais precisa de microhabitat quando comparada a insetos alados que utilizam a mesma estratégia de forrageamento, devido à sua maior dificuldade de movimentação na vegetação. No Panamá, Nentwig (1993) comparou as inflorescências de Lantana camara (Verbenaceae) e Palicourea guianensis (Rubiaceae), mostrando diferenças significativas na abundância e composição de famílias de aranhas. Ele argumentou que o tamanho da flor poderia ser uma das variáveis responsáveis por estas diferenças, mas não realizou testes que comprovassem esta hipótese.

O efeito das características estruturais do ambiente na seleção de microhabitat foi demonstrado para várias espécies de aranhas (veja Uetz 1991). Stratton (1979) comparou as espécies de aranhas presentes em três espécies de coníferas e sugeriu que as diferenças na arquitetura entre as árvores era o principal fator que determinava a presença ou a ausência de algumas espécies. É possível que diferentes famílias de aranhas possam utilizar diferentes espécies de plantas, de acordo com suas necessidades específicas. Por exemplo, grandes araneídeos e tetragnatídeos tendem a requerer grandes espaços para construção de suas teias (Uetz et al. 1978, Greenstone 1984), enquanto que aranhas não construtoras de teia devem ocorrer em folhagens mais densas (Hatley e MacMahon 1980, Robinson 1981, Scheidler 1990, Uetz 1991).

A distribuição de tamanhos das aranhas também deve estar condicionada indiretamente às características específicas do habitat, uma vez que a densidade e a composição das espécies envolvidas podem influenciar o resultado de interações entre indivíduos que são atraídos para estes locais. Além disto, a taxa de predação entre aranhas deve ser mais alta em locais com baixa complexidade estrutural devido a uma menor disponibilidade de refúgios nestes locais para aranhas de menor porte que poderiam ser mais facilmente detectadas por aranhas maiores (Gunnarsson 1985). Por outro lado, aranhas de maior porte podem ficar mais vulneráveis à predação por aves, e deve haver uma forte pressão de seleção para escolherem ativamente locais de refúgio apropriados (Waldorf 1976, Askenmo 1977, Gunnarsson 1990,1996).

No presente estudo, avaliaram-se as hipóteses de que a estrutura física do habitat deve influenciar a abundância, a estrutura de famílias e a distribuição de tamanhos entre espécies e em diferentes partes das plantas. Especificamente este estudo analisa o efeito de algumas variáveis da arquitetura de ramos vegetativos e inflorescências na distribuição de aranhas em vegetação arbustiva de uma área do cerrado brasileiro, divididos nos três capítulos subsequentes. No capítulo 2 descrevem-se diferenças na distribuição de aranhas entre sete espécies de plantas avaliando o efeito da complexidade estrutural de ramos vegetativos. Neste capítulo também são descritas as diferenças na composição de famílias e distribuição de tamanho corporal de aranhas em três espécies de plantas com diferentes níveis de complexidade estrutural de ramos. No capítulo 3, a distribuição de aranhas é comparada entre diferentes tipos de ramos (reprodutivos vs. vegetativos) dentro de uma mesma espécie de planta. Neste capítulo, também são avaliadas diferenças entre ramos vegetativos e inflorescências em quatro espécies de plantas com relação a abundância, composição em famílias e distribuição de tamanho corporal de aranhas. No capítulo 4, os efeitos da cor e arquitetura das inflorescências de diferentes espécies de planta são avaliados em relação à abundância e composição de famílias das aranhas que visitam flores. As variáveis estruturais das inflorescências usadas neste capítulo foram: tamanho, forma e complexidade estrutural das inflorescências, número de flores abertas bem como o tamanho e a cor das flores de 14 espécies de plantas arbustivas. No capítulo 5 são feitas as considerações finais resultantes das discussões encontradas nos três capítulos que o antecedem.

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CAPÍTULO 2

PLANT STRUCTURE AND DISTRIBUTION OF FOLIAGE-DWELLING SPIDERS

ABSTRACT

The distribution of foliage-living spiders was compared among seven plant species with different levels of structural complexity, described as the number of leaves per branch volume unit. Spider abundance among plant species was positively correlated to the structural complexity of their branches. Structurally more complex artificial branches placed on Baccharis dracunculifolia, Diplusodon virgatus, and Microlicia fasciculata attracted more spiders than less complex ones, when both biomass and texture effects are isolated. The size distributions of plant-dwelling spiders were similar among vegetative branches of plant species with different levels of structural complexity. Spider family structure differed between vegetative branches of three plant species, which had different levels of foliage density. Oxyopidae and Salticidae were more abundant on branches of the plant species with more density of leaves, B. dracunculifolia. On plant species with lower density of leaves, D. virgatus and B. gardneri, anyphaenids were the dominant family. Field data suggest that the structural complexity of plants may the most important factor determining the abundance of plant-dwelling spiders on the study area, and that spider families differ in microhabitat choice. The effect of refuge availability on differences of spider family structure is discussed.

INTRODUCTION

Plant structural complexity, the architectural arrangement of biomass in space, has been pointed as one of the main factors that determine the diversity and abundance of plant-dwelling spiders (Uetz 1975, Hatley and MacMahon 1980, Greenstone 1984, Scheidler 1990, Hurd and Fagan 1992, Gunnarsson 1990, 1996). Although causal mechanisms remain obscure, some variables have been proposed to explain this pattern, such as prey abundance (Allen et al. 1975, Hurd and Fagan 1992, Nentwig 1993), availability of refuges against predators (Askenmo et al. 1977, Gunnarsson 1996), and smoother microclimate conditions (Foelix 1996, Evans 1997, Henschell and Lubin 1997). Robinson (1981) proposed that the abundance of spiders be directly related to the structural complexity of plants, when described as a function of foliage density and leaf surface area, the latter being indirectly estimated by biomass. A positive influence between vegetation structure and spider abundance was demonstrated through foliage density of the big sage Artemisia tridentata (Hatley and MacMahon 1980), density of needles of the spruce Picea abies (Gunnarsson 1990), and leaf surface area of different species of Eucalyptus (Evans 1997). However, these studies were restricted to comparisons within a particular plant species or a few plant species of the same genus. In addition, the effect of biomass is normally confounded with the effect of branch structural complexity on spider density.

Spiders form a very diverse group, and several species may actively choose favourable microhabitats (Turnbull 1973, Foelix 1996). Their requirements for structural characteristics of microhabitats can change among families, since they differ in relation to hunting strategies, refuge and reproductive behavior, and morphological and physiological features as visual acuity, tolerance to sunlight and shade, moisture and thermal conditions (Turnbull 1973, Uetz et al. 1978, Foelix 1996). Thus, spider family distribution could be associated with characteristics of the microhabitat such as leaf size and foliage density (Hatley and MacMahon 1980, Robinson 1981, Scheidler 1990, Mason 1992), features that vary among different plant species.

Larger ones frequently prey upon small spiders, and higher spider densities enhance both the probability of inter-individual encounters and the frequency of interactions (Provencher and Vickery 1988, Polis et al. 1989, Hurd and Eisenberg 1990). If the structural complexity of plants and the presence of inflorescences influence the density of spiders in branches, a range of body sizes of spiders should indirectly be conditioned by microhabitat characteristics.

In this study, we examined the spider distributions among plant species of different genus or families. Specifically we tested (1) the structural complexity hypothesis proposed by Robinson (1981) - suggesting that spider abundance is directly related with plant structural complexity, a result of foliage density and leaf surface area; (2) whether family and body size distributions of spiders change among plants with different levels of structural complexity.

MATERIALS AND METHODS

This study was carried out in an old-field site at the Estação Ecológica do Panga, located 40Km South from Uberlândia, SE Brazil (19°09'S, 48°23'W). The ecological station includes plant formations such as Cerrado (a type of savannah), old fields and forest (Schiavini and Araújo 1989).

Seven plant species that were abundant in the study area and with different foliage density levels were sampled to test structural complexity effect on spiders abundance. Branches (one per plant) of Baccharis dracunculifolia (Asteraceae) (n = 30), Bidens gardneri (Asteraceae) (n = 21), Chromolaena laevigata (Asteraceae) (n = 20), Diplusodon virgatus (Lythraceae) (n = 21), Microlicia euphorbioides (Melastomataceae) (n = 25), Microlicia fasciculata (Melastomataceae) (n = 15), and Vochysia tucanorum (Vochysiaceae) (n = 14), were collected from December 1997 to February 1998. All sampled plants had between 1 and 2 m high. Each branch was carefully enclosed in a plastic bag and cut at about 40 cm from its tip. The plastic bags were sealed in the field, and filled with CO_2 at the laboratory before examination. The spiders were separated, and fixed in 70% ethanol.

A component of plant structural complexity can be described as a result of plant branching (see Kuppers 1989). Here, as a measure of this component we used a foliage density index (FDI), defined as the ratio between the number of leaves and branch volume. The number of leaves was standardised to prevent the effect of branch volume on spider abundance (see Scheidler 1990). Ten branches (one per individual) were sampled from each plant species, and the number of leaves per branch recorded. From each branch, the leaf surface area was estimated from ten leaves with a digital scanner. For simplicity, we assumed that differences of the number of leaves per branch and leaf surface area within plant species were smaller than those between them. Thus, we considered only the mean values of these variables for each plant species. Branch volume was estimated from measures of the three dimensions of the branch, following the method proposed by Hacker and Steneck (1990). As FDI was positively correlated with mean leaf surface area ($r = 0.995$, $p < 0.001$), we used only mean FDI to test the effect of plant structural complexity on spider abundances.

The relation of spider abundance and leaf surface area was tested with a randomised blocks experimental design. Plant species were Baccharis dracunculifolia, M. fascicular and D. virgatus used as block. The structural complexity of their branches was manipulated by replacing natural branches with artificial ones. The experimental set-up consisted of wire and plastic models, with 24 secondary branches and leaf models made of cloth, to prevent the effects of both chemical components and texture of the natural branches. High and low foliage density were used. For the high foliage density treatment, each secondary branch had four model leaves, totalling 96 model leaves (Figure 1A). In the low foliage density treatment, two model leaves were attached to 12 secondary branches, whereas the remaining branches had no leaves (Figure 1B) totalling 24 model leaves. In the high complexity branches, each model leaf had an area of 1.5 cm^2 whereas in the low foliage density ones each model leaf had 6.0 cm^2. Thus, total leaf surface area and biomass were kept constant in both treatments. For each individual plant, a natural primary branch was cleared of leaves and of secondary branches, to be used as support. An artificial branch was tied to the support branch with a thin wire. Thirty-two artificial branches of each treatment were attached to different plants, 24 plants were used for B. dracunculifolia and M. fasciculata, 12 in each treatment, and 16 in D. virgatus (eight in each treatment). One week later, the artificial branches were collected between 17h00-19h00 to equalise possible effects of weather on spider activity.

Family structure and body size distribution

To evaluate the relationship between plant structural complexity and family and body size distribution of spiders, 70 branches from each of three plant species were sampled. The plant species sampled were B. dracunculifolia with higher foliage density, FDI = 28.82 ± 1.50 (mean ± 1 SD), D. virgatus with intermediate foliage density FDI = 10.34 ± 1.28, and B. gardneri with lower foliage density FDI = 1.37 ± 2.03. They were significantly different in foliage density ($F_{2,27} = 98.49$, $P < 0.001$). The abundance of each family was compared in the high, intermediate and low FDI plant species.

The spiders are usually classified into two large groups: wandering and web-building spiders due to differences of behavior on the use of silk to capture prey (Turnbull 1973). In this study, the web-builders Araneidae, Theridiidae, and Dictynidae composed only 11.3% of the individuals, and therefore were not separated into families. The groups of spiders used in the frequency analyses were Anyphaenidae, Oxyopidae, Salticidae, Thomisidae, and web-builders. The remaining families represented only 4.8% of the sample. Spider body sizes were estimated as their total body length (distance between chelicerae and spinners, precision = 0.1mm).

Data analysis

The relationship between spider abundance and foliage density (FDI) was analysed with linear regression. Each replicate consisted of the mean number of spiders per branch in each species. The experiment using artificial branches with two structural complexity levels was evaluated with a 2-way ANOVA. Residuals of each analysis were graphically checked for non-normality, and data were $\log_{10}$ transformed to comply with the assumption of normal distribution and equal variances. G–tests were used to test differences on family distribution, and two-sample Kolmogorov-Smirnov tests were used to compare the size distribution of spiders among the three plant species with different structural complexity levels (Sokal and Rohlf 1995).

RESULTS

The mean number of spiders per branch was linearly related to the structural complexity index ($y = -1.723 + 0.334 x_i$, $P = 0.014$, $r^2 = 0.73$) (Figure 2). The most abundant spider families in the sampled plant species were Anyphaenidae (23.1%), Oxyopidae (20.0%), and Salticidae (18.5%). The remaining families were Miturgidae, Thomisidae, and Pisauridae, and 29.2% were web-builder spiders (Araneidae, Theridiidae, Dictynidae, and Scytodidae).

The mean number of colonising spiders on model branches from the three plant species was significantly larger in the more complex branches (0.625 ± 0.042) than in the less complex ones (0.222 ± 0.048), ($F_{1,2} = 522.1$, $P = 0.002$).

A total of 170 spiders were recorded on branches of B. dracunculifolia, D. virgatus and B. gardneri. Several spiders were juveniles and were not possible to be identified to genus or species levels. The species and genus recorded on the three plant species are presented on Table 1. The size distribution of spiders was not significantly different among branches sampled from the three plant species: B. dracunculifolia, and D. virgatus (KS = 0.079, $P > 0.05$); B. dracunculifolia and B. gardneri (KS = 0.039, $P > 0.05$); D. virgatus and B. gardneri (KS = 0.079, $P > 0.05$) (Figure 3). Family composition differed among the three plant species ($G_8 = 23.565$, $P < 0.001$); when each family was tested separately, the frequency of oxyopids and salticids were significantly different from that expected by chance (Table 2). On D. virgatus and B. gardneri, Anyphaenidae was the most abundant family with 50.0% and 41.3% (Table 2) from the total number of spiders recorded in these plant species.

DISCUSSION

Our study demonstrated that the abundance of spiders in plants is linearly related with the foliage density. Most of the variance of spider abundance (73%) was explained only by a component of branch structural complexity described here. The model proposed by Robinson (1981) regards the number of leaves and total leaf surface area - the latter as an estimate of biomass - as the factors that determine spider abundance. Our results showed that leaf surface area was negatively correlated with number of leaves. Although we did not directly estimate the effects of biomass and texture, the experiment using plastic vegetative branch models suggested that foliage density had a strong effect even when these effects are isolated. Thus, at least in smaller spatial scale, biomass and texture may have less importance on spider abundance.

Studies emphasizing the relationship between arthropod body size and vegetation structure are scarce and restricted to a few systems. Gunnarsson (1990) showed that spider abundance in needle-thin spruce branches decreased when compared to needle-dense branches, but the size distribution was not affected. In our system, the size distribution of spiders on plant species with distinct levels of foliage density was also similar. Branches less structurally complex attracted a lower numbers of spiders, and less inter-individual interactions may occur. On the other hand, more complex branches have more refuges and barriers, reducing the probability of inter-individual encounters and possible negative interactions among them (see Provencher and Vickery 1988). Alternatively, differences in branch structural complexity within the range analyzed in this study may have not been large enough to result in great size asymmetry.

Family structure differed among branches of B. dracunculifolia, D. virgatus and B. gardneri. When the distribution of each family was separately analyzed the distribution of Oxyopidae and Salticidae on the three plant species was significantly different from that expected by chance. In addition, Anyphaenidae was the dominant family on plant species with lower foliage density, D. virgatus and B. gardner, with relative abundance of 0.42 and 0.41 respectively (see Table 2). On the plant species with higher foliage density, B. dracunculifolia, we observed no dominant spider family. Scheidler (1990) suggested that differences in the spider fauna of different plant species indicate the existence of spider associations for specific habitat types. The narrower diet of some spider families can constrain their distribution (see Nyffeler et al. 1994), while predation can be the most important factor determining the distribution of species of other families (see Provencher and Vickery 1988, Ehmann and MacMahon 1996). Spiders are frequently preyed by birds (Askenmo et.al. 1977, Gunnarsson 1983) and arthropods such as mantids (Moran and Hurd 1994), wasps, and other spiders (Wise 1993, Nyffeler and Sterling 1994, Wise and Chen 1999). From the families recorded on vegetative branches of the three plant species evaluated in our study, only anyphaenids are regarded as nocturnal, spending the diurnal periods sheltered inside tubular retreats built of silk threads in the foliage, while the remaining families of wandering spiders are diurnal (see Comstock 1971). Thus, it is possible that anyphaenids can escape from visually oriented predators such as spiders (Salticidae, and Oxyopidae), birds, mantids and wasps on plants with low foliage density. Our results agree with the hypothesis that night–active groups such as clubionids and anyphaenids should differ in their distribution and requirements from oxyopids and salticids, which depend upon well–developed eyesight (see Wise 1993). However, further experiments are necessary to evaluate the effect of refuge availability on the distribution of some diurnal families as Thomisidae, Oxyopidae, and Salticidae on plants, compared with other nocturnal ones such as Anyphaenidae, Miturgidae, and Clubionidae.

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Table 1 – Spiders on branches of Bidens gardneri, Diplusodon virgatus, and Baccharis dracunculifolia. Identification could not always be made to genus or species level since many individuals were juvenile.

Family	Genus / Species
Salticidae	Thiodina sp., Frigga sp.
Oxyopidae	Oxyopes salticus, Hamataliwa sp1, Hamataliwa sp2.
Thomisidae	Misumenops pallida, M. pallens, Synaema sp., Tmarus sp.
Heteropodidae	
Anyphaenidae	Arachosia sp., Teudis sp.
Miturgidae	Cheiracanthium inclusum
Theridiidae	Episinus sp., Euryops sp., Dipoena sp.
Araneidae	
Dictynidae	Dictyna sp.

Table 2 – Absolute frequency of spiders per family on three plant species (df = 2). Numbers in parentheses are the percentage from the total of spiders in each plant species.

Family	B. dracunculifolia	D. virgatus	B. gardneri	χ^2	P
Anyphaenidae	19 (23.8)	26 (50.0)	19 (41.3)	1.53	0.465
Oxyopidae	21 (26.2)	5 (9.6)	1 (2.2)	24.89	< 0.001
Salticidae	19 (23.8)	8 (15.4)	9 (19.6)	6.17	0.046
Thomisidae	10 (12.5)	4 (7.7)	9 (19.6)	2.70	0.260
Web-buildings	10 (12.5)	4 (7.7)	6 (13.0)	2.80	0.247
Other	1 (1.2)	5 (9.6)	2 (4.3)		
Total	80	52	46		

Legends of Figures

Figure 1 – Design of model branches used as treatments. Branches more (A) and less (B) structurally complex were attached to pruned natural branches.

Figure 2 – Relationship between the mean number of spiders per branch and foliage density index (FDI). Line is the least square fit, bars indicate the standard deviation.

Figure 3 – Frequency of spiders in different size class on three plant species: (A) Bidens gardneri.; (B) Diplusodon virgatus; and (C) Baccharis dracunculifolia.

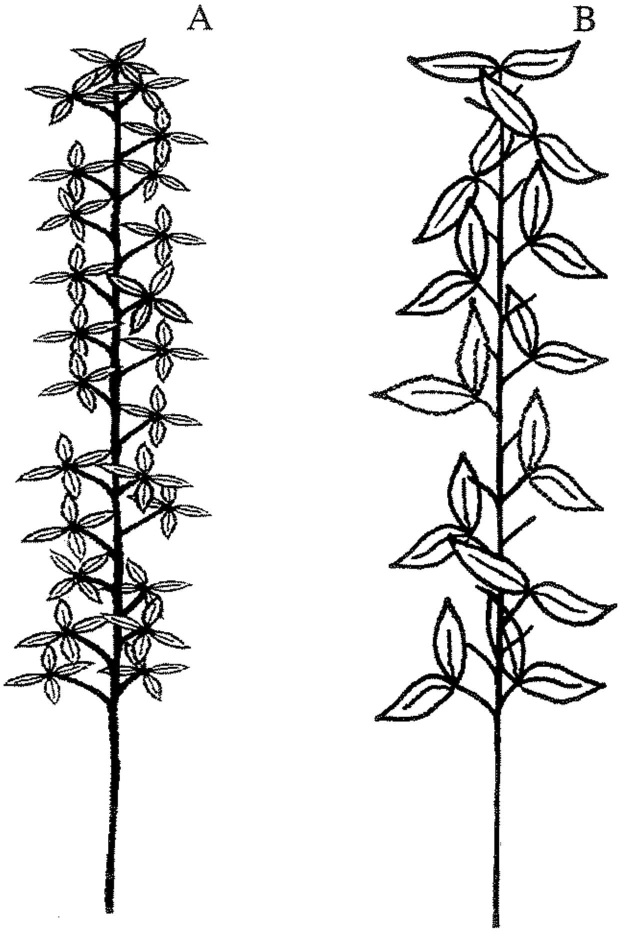

Figure 1

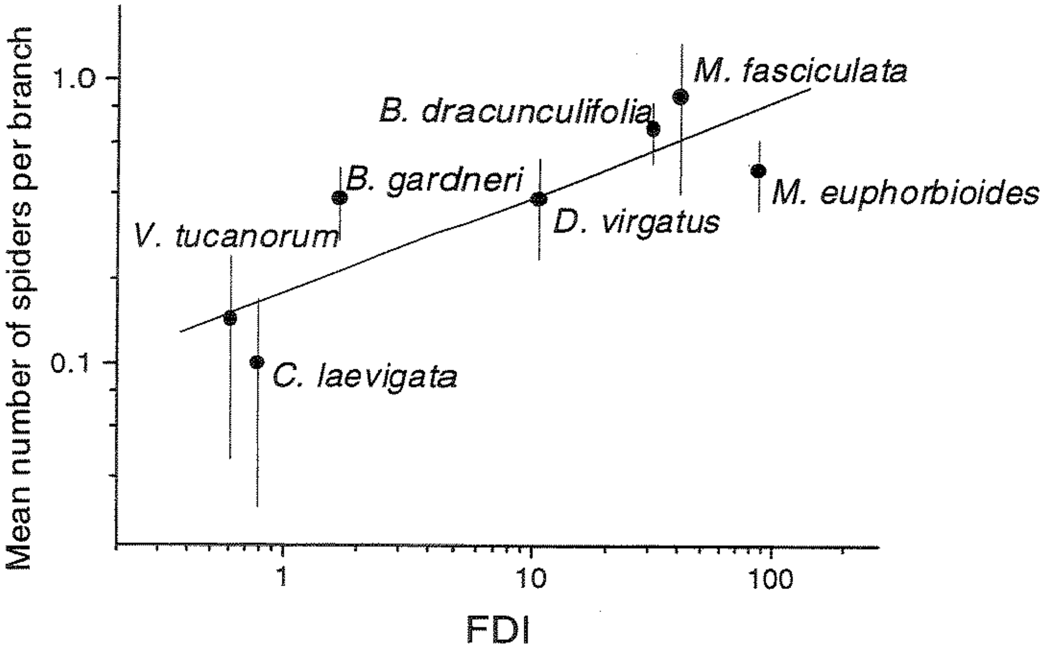
Mean number of spiders per branch
1.0
0.1
1
10
100
FDI
M. fasciculata
B. dracunculifolia
B. gardneri
M. euphorbioides
D. virgatus
V. tucanorum
C. laevigata

Figure 2

CAPÍTULO 3

Distribution of plant-dwelling spiders: inflorescences vs. vegetative branches

ABSTRACT

The distribution of foliage-living spiders was compared between inflorescence and vegetative branches of four plant species. Plant phenology had a strong effect on spider abundance. For all plant species, inflorescences attracted more spiders than vegetative branches. For most of the year, artificial inflorescence models on Baccharis dracunculifolia also attracted more spiders than non-manipulated vegetative branches. Wandering spiders (Anyphaenidae, Miturgidae, and Salticidae) occurred preferentially on artificial inflorescences relative to control branches. The frequency of thomisids, oxyopids and web–building spiders were not significantly different between inflorescence models and control branches. Thomisids occurred mainly (65%) during the flowering period of B. dracunculifolia, when control branches had flower buds. Artificial inflorescences also influenced the size distribution of spiders; larger spiders were more abundant on inflorescence models than on vegetative branches. The effect of spider density on size distributions was significant for spiders on inflorescences, but not on vegetative branches. Inflorescence models with lower spider density were more colonized by larger spiders than inflorescence models with higher spider density. The body size distributions can be density-dependent, and interactions among predators may influence the abundance and size distribution of spiders in favorable microhabitats. The hypothesis that habitat characteristics can influence the spider size distribution was supported, but a balance between habitat structural features and spider density seems to be critical in determining the size distribution of plant-dwelling spiders.

INTRODUCTION

Spiders exert a significant impact upon densities of herbivore insects (Wise 1993, Spiller and Shoener 1994, Riechert and Lawrence 1997), and have even been pointed as possible biological control agents in agrosystems (Riechert and Bishop 1990). Due to its interactions with herbivore and pollinator insects, spiders can also indirectly influence the amount of viable seeds produced by plants (e.g. Louda 1982, Aluri 1992, Ott et al. 1998). Nevertheless, the distribution of these predator arthropods on plants, especially between reproductive and vegetative branches, is poorly understood.

Plant-dwelling spiders are spatially segregated, and prey abundance, availability of predator–free refuges, and smooth microclimate conditions have been proposed to explain aggregative numerical responses of several species on plants (e.g. Askenmo et al. 1977, Hurd and Fagan 1992, Nentwig 1993, Gunnarsson 1996, Henschell and Lubin 1997). Inflorescences can be high-quality foraging sites for spiders, as they attract pollinators and other phytophagous insects (Louda 1982, Morse and Fritz 1982). In addition, spiders can also use floral structures as reproductive sites and for shelter (Nentwig 1993). Thus, an influence of plant phenology on the density of spiders on branches is expected. However, spider families may require distinct microhabitat structural characteristics (Hatley and MacMahon 1980, Robinson 1981, Scheidler 1990, Mason 1992), since families differ in morphological, physiological, and behavioral features such as visual acuity, tolerance to sunlight and shade, moisture, and thermal conditions, hunting strategies, refuge, and reproductive behavior (Turnbull 1973, Uetz 1977, Nyffeler and Sterling 1994, Foelix 1996). In this study we evaluated the effect of the presence of inflorescences on spider distribution. Specifically we tested whether (1) spider abundance, and

(2) family structure differs between inflorescences and vegetative branches.

Provencher and Vickery (1988) proposed a model where spiders spend most of their time in favourable patches. Conversely, when the expected energy balance is negative, spiders become marginal or floaters. In addition, larger spiders can have a greater ability to actively select microhabitats than the smaller ones (see Waldorf 1976). Thus, if inflorescences constitute high quality patches, and more and larger spiders are attracted to them, a segregation of distinctly-sized spiders would be expected, since larger spiders should occur in sites with low spider density since they can prey upon small spiders (Turnbull 1973, Gunnarsson 1985, Polis et al. 1989). Thus, we also tested (3) whether size distribution is similar between inflorescences and vegetative branches, and (4) the effect of density on size distribution of spiders on inflorescences and vegetative branches.

MATERIALS AND METHODS

This study was done between October 1997 and November 1998 in an old–field area at the Estação Ecológica do Panga, south of Uberlândia, Minas Gerais State, SE Brazil (19°9'S; 48°23'W). The ecological station includes savannah–like Cerrado, old fields, and forest (Schiavini and Araújo 1989). This area is markedly seasonal, with a well-defined dry season between May and September and a wet season between December and February (see Barbosa, 1997).

The hypothesis that spider abundance differed between inflorescences and vegetative branches was tested on four very common and widespread plant species in the study area: Microlicia helvola (Melastomataceae), Diplusodon virgatus (Lythraceae), Baccharis dracunculifolia (Asteraceae), and Bidens gardneri (Asteraceae). Sampling was done from January to May 1998 at the beginning of the flowering period of each plant species, when both flowering and vegetative branches could be found. An inflorescence or a vegetative branch of the same length was collected from each individual plant. Twenty inflorescences and twenty vegetative branches were sampled from each plant species in each of two sites apart about 1000m from each other. Each branch was carefully enclosed in a plastic bag, sealed and cut at 40 cm from the distal end. The plastic bags were taken to the lab, and filled with CO_2 before examination.

The effect of inflorescences on spider abundance, family structure, and size distribution was also tested with artificial inflorescences made of cloth, plastic, and wire, attached to plant branches. Only B. dracunculifolia was used in this experiment, to avoid possible influence of other factors on the results. Inflorescence models were white and purple; containing 30 flowers, conic shaped, with 3.2cm width and 2.0cm height, in two secondary branches. An artificial inflorescence was attached with thin wire to a treatment branch, which was previously partially pruned to have a total number of secondary branches similar to that of the vegetative branches (controls). In each trial, 20 model inflorescences were kept for eight days in the field on different individuals (one model for each plant) of B. dracunculifolia. Afterwards, the treatment and one unmanipulated branch (control) from the same plant were collected as described above. Inflorescences were available for spider colonisation during the year, by placing artificial inflorescences on B. dracunculifolia branches at two-month intervals. Two trials per month (n = 14) were made in seven different dates: October and December 1997, February, April, June, August and November 1998. The sampling unit was each trial, and the total number of spiders in 20 branches was used in the analysis. The numbers of spiders on inflorescence models and vegetative branches were recorded to compare the spider size distribution among branches with different density levels. All spiders were separated, identified, and their body length measured under a steroscopical microscope as the distance between chelicerae and spinners (precision = 0.1mm). The wandering spiders were separated by family. Web-building spider families Araneidae, Theridiidae, and Dictynidae composed only 7.7% of the individuals recorded on B. dracunculifolia (see Table 3) and due their similarities in the use of silk and requirements to open spaces to attach their webs, these spiders were grouped.

Data analysis

A mixed–model ANOVA was used to test the type of branch, natural inflorescences and vegetative, and plant species effects on spider abundance. Because of large numbers of zeros, spiders on branches sampled within a plant species and in the same site were pooled to assess the normality of data. Spider abundance on treatment and control branches was compared within each month with Student's *t* test (see Box et al. 1978). Each replicate consisted of the total number of spiders per site (trials) in each species. Residuals of each analysis were graphically checked for non-normality and variance trends. Differences on the abundance of spider families, and the size distribution between inflorescence models and vegetative branches were compared using G-tests, and density effects on size distribution with Kolmogorov-Smirnov tests (see Sokal and Rohlf 1995).

RESULTS

There were significantly more spiders on natural branches with inflorescences than on vegetative ones (Table 1, Figure 1). The most common families were Anyphaenidae, Salticidae and Thomisidae. There was also a higher abundance of spiders on model inflorescences compared to vegetative branches along the year, except in April and November (Figure 2). There were many juvenile spiders present on natural and artificial inflorescences and vegetative branches, and only some could be identified to genus (Table 2). The most common families recorded along the year on inflorescence models were Anyphaenidae (40.5 %), Salticidae (18.8 %), Thomisidae (14.8 %), and Miturgidae (14.6 %), from a total of 378 spiders against 205 spiders on control branches. Family composition also differed between treatment and control branches ($G_5 = 18.04$, $\underline{P} = 0.003$). When analysed separately, Anyphaenidae, Salticidae, and Miturgidae occurred preferentially on treatment over control branches, while the frequency of oxyopids, thomisids, and web-building spiders was not different between branch types (Table 3). Anyphenidae peaked in December, with intermediate values between February and June, and a strong decline in August. Miturgidae were rare in October and December, peaking in August (Figure 3). The trials done in April overlapped with the flowering period of B. dracunculifolia. We observed an increase in the abundance of thomisids (65% of the total), resulting in an increase of 43.4% in the number of spiders recorded on that month (see Figure 3). From all thomisids recorded during the flowering time, 44% were adult and subadult individuals.

Spider size distribution differed between inflorescence models (treatment), and vegetative branches (control) ($G_9 = 30.093$, $\underline{P} < 0.001$). In treatment branches there were larger spiders, when compared to the controls (Figure 4). When the size distribution on inflorescence models was analysed separately, the difference was not significant between treatment branches with one and two spiders (KS = 0.130; P = 0.388) but was significant between one and three or more spiders per treatment branch (KS = 0.254; P = 0.013) and between two and three or more spiders per treatment branch (KS = 0.207; P = 0.021) (see Fig. 5D, E, F). However, no significant association was found on vegetative branches: size distribution was similar between one and two spiders per branch (KS = 0.106; P = 0.925), between one and three or more spiders per branch (KS = 0.224; P = 0.346), and between two and three or more spiders per branch (KS = 0.126; P = 0.978) (see Fig. 5A, B, C).

DISCUSSION

This study demonstrated that the phenological state of the plant affects spider abundance within plant species, as natural inflorescences attracted more spiders than vegetative branches. Spiders can actively choose favourable microhabitats and, as predicted, availability of prey and refuge probably are the main factors influencing their distribution (e.g., Morse and Fritz 1982, Morse 1986, Riechert and Gillespie 1986). Spiders also responded to inflorescence models, since the their abundance were higher on inflorescence models than vegetative branches, except in April when Baccharis dracunculifolia flowered, and in November when the total number of spiders recorded was the lowest of the year. The flowering time for all plant species in the study area is restricted to the rainy season, between November and April (see Barbosa 1997). However, spiders are attracted to inflorescence models even in the dry season, when all plant species are vegetative. Thus, it is possible that at least some spider species are not necessarily associated with the inflorescences, but respond opportunistically to favourable conditions provided by experimental inflorescences. Although we did not record the number of potential prey attracted to both branch types, inflorescence models may attract more insects than vegetative branches (see Bernays and Chapman 1994). However, artificial inflorescences may not attract the same amount of prey as natural ones do, since these models lacked scent and taste, critical clues involved in the attraction of several insects. Furthermore, prey availability may not be a limiting factor to spiders on vegetative branches (see Wise 1993). Alternatively, as in natural flowers, inflorescence models can be predator-free sites or provide smoother microclimate conditions for the spiders. Thus, aggregative responses of flower visiting-spiders could be more related to specific habitat features than to prey abundance (see Riechert and Tracy 1975, Greenstone 1984, Provencher and Vickery 1988).

Anyphaenidae, Miturgidae, and Salticidae occurred mainly on inflorescence models relative to vegetative branches. On the other hand, the occurrence of oxyopids, thomisids, and web–building spiders was not significantly different between inflorescence models and vegetative branches (Table 2). Oxyopids and web-building spiders were relatively rare on both model and natural inflorescences, but the occurrence of thomisids must be evaluated with caution. Higher thomisid occurrence (65%) overlapped with the flowering period of B. dracunculifolia. Thus, these spiders may have been attracted to the control branches, which had natural flowers at that time, influencing the results. Several species of Thomisidae are usual flower inhabitants, and both visual cues and prey abundance is crucial for these spiders to select hunting sites (Morse 1988, Greco and Kevan 1994, Foelix 1996). Part of the thomisids attracted to B. dracunculifolia, during the flowering time, could be the consequence of a synchrony of their life cycles with plant phenology, since natural inflorescences could provide a more abundant food supply. However 44% of them were larger spiders (adults and subadults). Natural inflorescences could attract more insects than artificial ones, and the presence of prey could be the main factor influencing the choice decision, specifically for thomisids, to natural inflorescences (see Morse and Fritz 1982). Some features that were not evaluated here but that may help to discriminate between the two types of inflorescences (artificial vs. natural) could be critical factors in attracting these spiders.

Our results support the general hypothesis that habitat structure can influence body size distribution in spiders (e.g. Morse et al.1985, Uetz 1991, Gunnarsson 1990, 1996, Nyffeler et al. 1994), but suggest that an interaction between habitat-quality and density is plausible. Branch type (inflorescence models vs. vegetative branches) influenced the size distribution of spiders on B. dracunculifolia. Larger spiders occurred more frequently on artificial inflorescences than on vegetative branches. When spider size distribution was compared among different levels of spider density on inflorescence models, most small spiders were present on branches with more than three spiders, and larger spiders occurred preferentially on branches with only one or two individuals. However, the effect of density was not significant when tested on vegetative branches of this plant species. Caraco and Gillespie (1986) proposed that ambush spiders use different strategies of movement depending on the habitat quality. Larger spiders could be spending most of their time foraging and sheltering in inflorescences, but not on vegetative branches. Intraguild predation may be one of the most important density-dependent mortality factors for wandering spiders (Wise 1993). Moran and Hurd (1994) showed that when the density of mantids and other spiders was experimentally increased, small spiders can emigrate to escape, reducing the chances of an encounter with potential predators. If so, larger ones can prey upon small spiders, emigrate from sites with a high density of potential predators, or avoid getting near larger spiders. Thus, the effect of density on spider size distribution may also depend on habitat quality reflecting, for instance, refuge or prey availability. A balance between structural characteristics and spider density should, at least in part, determine the size range of spiders attracted to a specific habitat. However, further empirical and experimental studies concerned with manipulation of spider density on high and low quality patches will be needed to evaluate this hypothesis.

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Table 1 – Two-way analysis of variance for the abundance of spiders on Baccharis dracunculifolia, Microlicia helvola, Diplusodon virgatus and Bidens gardneri (plant species) and between inflorescences and vegetative branches (branch type).

Source	d.f.	MS	F	P
Plant species	3	0.357	1.920	0.205
Branch type	1	3.564	19.161	0.002
Plant species vs. branch type	3	0.172	0.925	0.472
Error	8	0.186		

Table 2 – Wandering spiders recorded on inflorescences and vegetative branches of Baccharis dracunculifolia, Microlicia helvola, Diplusodon virgatus and Bidens gardneri.

Family	Species
Anyphaenidae	Arachosia sp., Teudis sp.
Miturgidae	Cheiracanthium inclusum
Salticidae	Chira sp., Thiodina sp., Frigga sp.,
Oxyopidae	Oxyopes salticus, Hamataliwa sp1, Hamataliwa sp2, Peucetia sp.
Thomisidae	Misumenops pallens, Misumenops pallida, Synaema sp., Misumena sp., Tmarus sp.

Table 3 – Absolute frequency of spider families on inflorescence models and control vegetative branches. The wandering spiders were separated into family level, web-building spider families composed by (Araneidae, Theridiidae, Dictynidae) and the remaining species were grouped into two others groups, Web-builders and Others respectively.

Group	Inflorescence models	Vegetative branches	χ^2	P
Anyphaenidae	153	71	30.02	< 0.001
Miturgidae	55	16	21.42	< 0.001
Oxyopidae	18	21	0.231	0.631
Salticidae	71	33	13.89	< 0.001
Thomisidae	56	40	2.67	0.102
Web-builders	23	22	0.022	0.881
Other	4	1	-	-
Total	380	204		

Legends of Figures

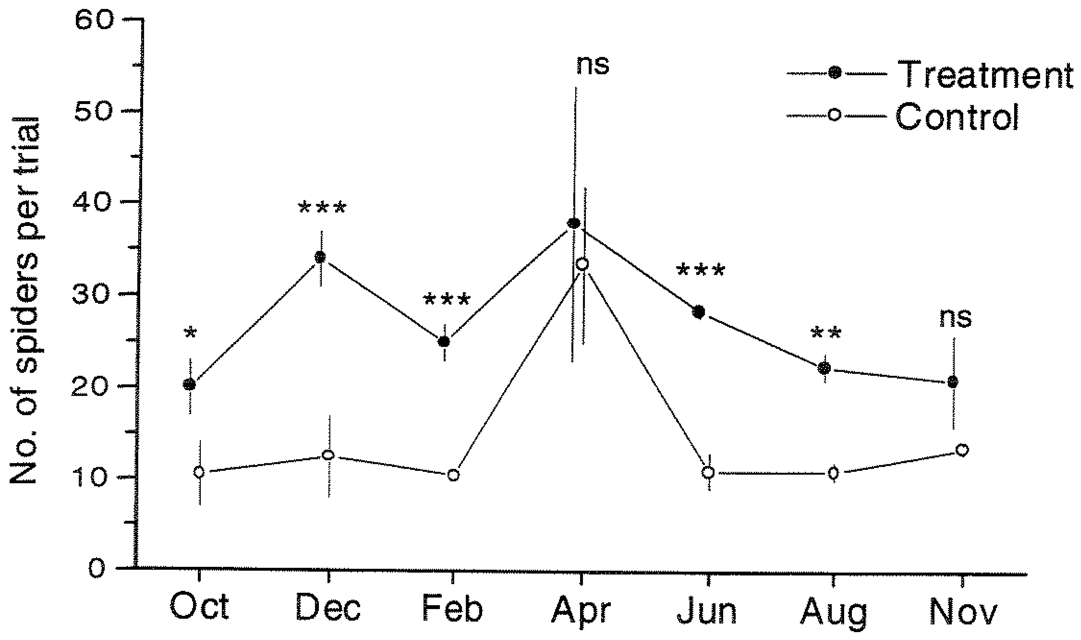
Figure 1 – Number of spiders per trial on natural inflorescences and vegetative branches of four plant species: MIC = Microlicia helvola, BAC = Baccharis dracunculifolia, DIP = Diplusodon virgatus, and BID = Bidens gardneri. Bars represent means and standard errors.

Figure 2 – Number of spiders per trial on inflorescence models (treatment) and vegetative branches (control) in different periods of the year. Bars represent means and standard errors. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns = not significant.

Figure 3 – Abundance of spiders from different families on inflorescence models placed on Baccharis dracunculifolia in different times of the year. Arrow indicates the flowering time of the plant species.

Figure 4 – Spider size distributions on inflorescences models (treatment) and vegetative branches (control) from Baccharis dracunculifolia.

Figure 5 – Spider size distribution on: (A, B, C) vegetative branches (control), and (D, E, F) inflorescence models (treatment), in three density classes: one (A, D), two (B, E) and three or more (C, F) spiders per branch of Baccharis dracunculifolia.


60
50
40
30
20
10
0
No. of spiders per trial
Oct
Dec
Feb
Apr
Jun
Aug
Nov
Treatment
Control
*
***
***
ns
***
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ns

Figure 2

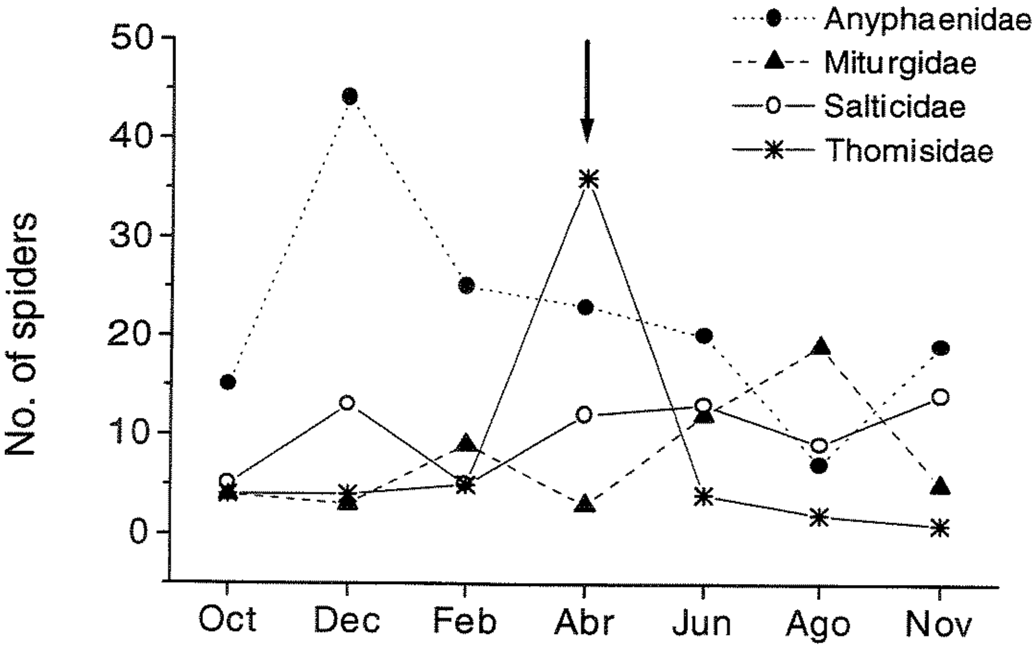
Anyphaenidae
Miturgidae
Salticidae
Thomisidae
No. of spiders
50
40
30
20
10
0
Oct
Dec
Feb
Abr
Jun
Ago
Nov

Figure 3

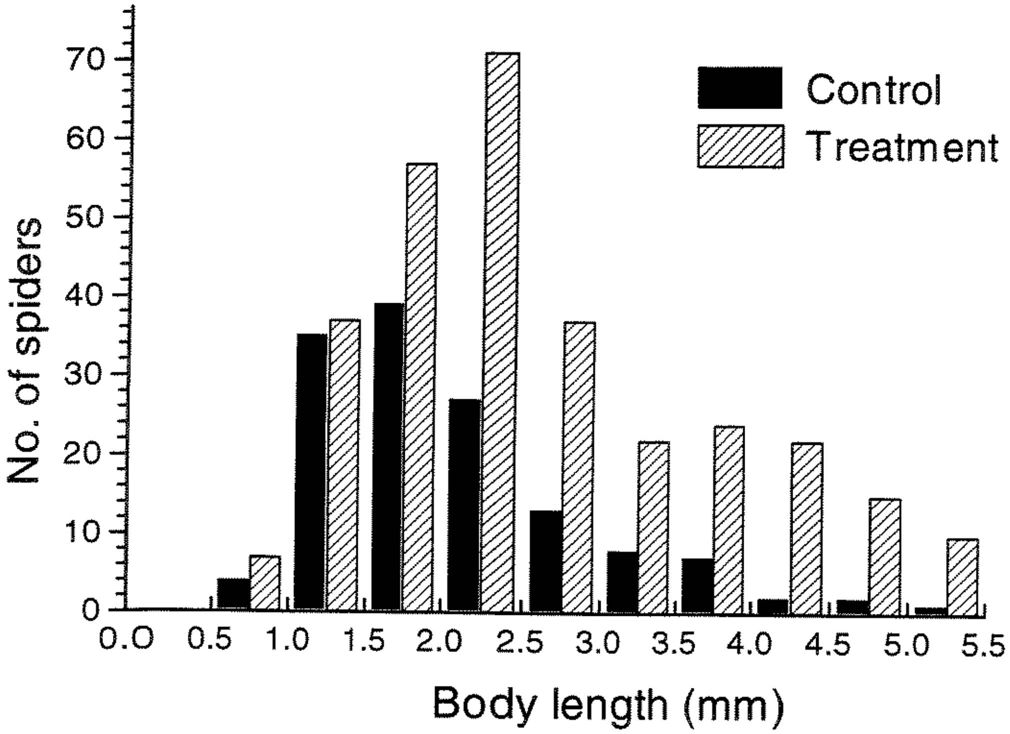
Control
Treatment
No. of spiders
0
10
20
30
40
50
60
70
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
Body length (mm)

Figure 4

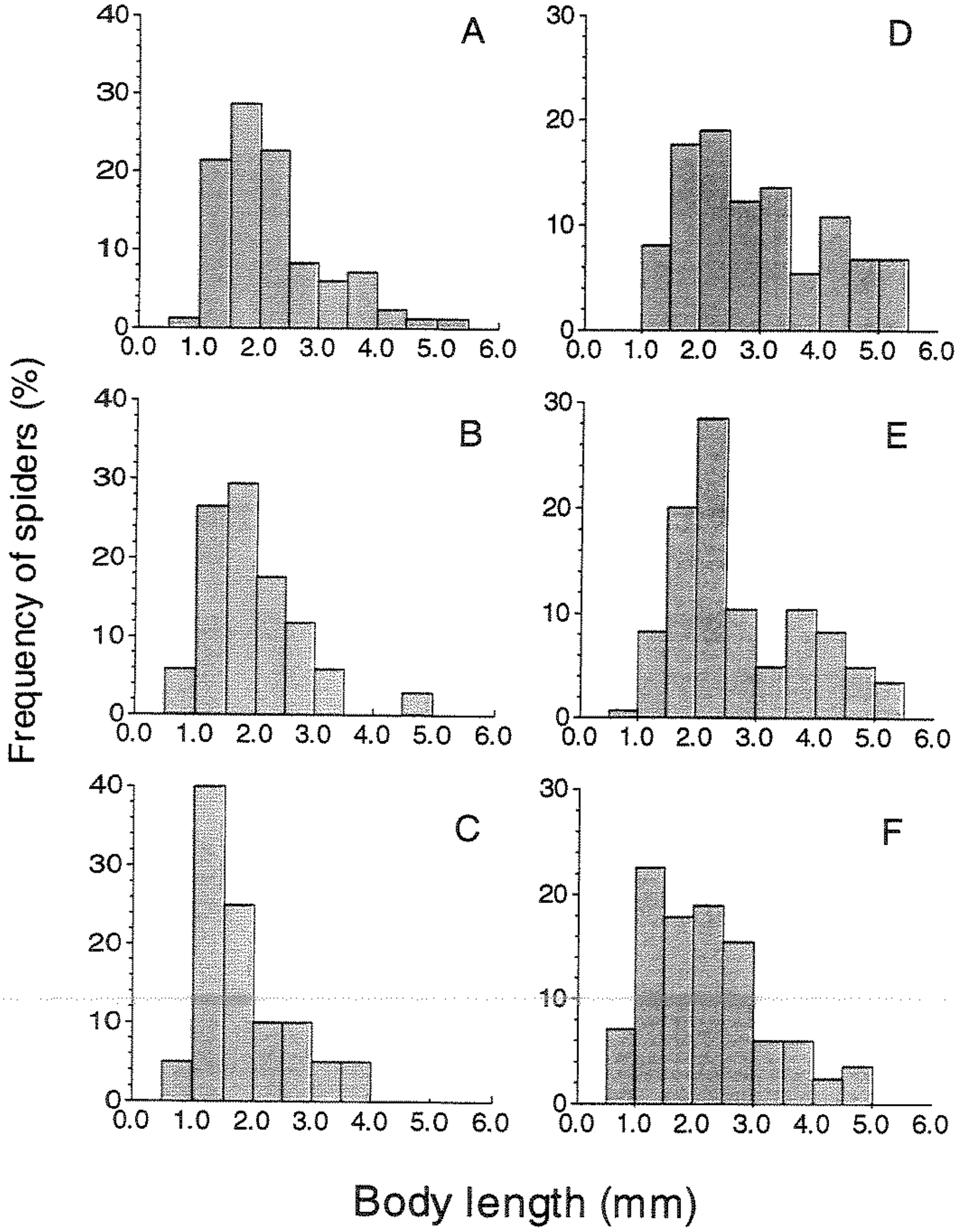
A
B
C
D
E
F
0
10
20
30
40
0.0
1.0
2.0
3.0
4.0
5.0
6.0
Frequency of spiders (%)
Body length (mm)

Figure 5

CAPÍTULO 4

IS THE DISTRIBUTION OF FLOWER-DWELLING SPIDERS INFLUENCED BY DIFFERENT TYPES OF INFLORESCENCES?

ABSTRACT

The distribution of spiders on inflorescences was compared among 14 plant species. We analysed size, flower colour and size, number of flowers, and number of nectar-secreting flowers in the inflorescences. The number of nectar-secreting flowers and flower size explained most of the variance (72% of total spider abundance among inflorescences). On the other hand, both the number of flowers and inflorescence size contributed to explain the frequencies in which different spider families occur. The abundance of salticids was positively correlated with the number of flowers, whereas anyphaenids, miturgids, and oxyopids were most common on large inflorescences. However, thomisids were more common on yellow inflorescences, and with larger flowers. The colour of artificial inflorescences influenced the abundance of thomisids and anyphaenids, whereas miturgids were influenced by inflorescence type, being more abundant on umbel inflorescences. Both natural and artificial inflorescences with large flowers sheltered larger spiders than inflorescences with small flowers. We suggest that architectural characteristics strongly influence the size distribution of spiders. Different inflorescence characteristics can influence the abundance, family composition and size distribution of flower-dwelling spiders. Possible effects of these variations on the distribution of spiders and on plant seed production are also discussed.

INTRODUCTION

The distribution of spiders may result from differential growth and reproduction rates in favourable habitats, or from active choice of such habitats (e.g. Robinson 1981, Janetos 1986, Morse 1988, Henschel and Lubin 1997). Several spiders actively choose microhabitats, and prey abundance is one of the most important variables influencing habitat selection (Morse 1981, Morse 1986, Riechert and Gillespie 1986, Nentwig 1993, Wise 1993). Specifically for plant-dwelling spiders, other factors such as branch size, number of flowers, and inflorescences can increase the availability of refuge sites against predators and/or favourable climate conditions (Hatley and MacMahon 1980, Robinson 1981, Provencher and Vickery 1988, Scheidler 1990, Gunarsson 1990, 1996, Morse 1993).

Abundance of potential prey for spiders can change among different inflorescence types, since size and number of flowers of inflorescences, and form, size, odour, and colour of their flowers, influence the abundance and size of visiting insects (De Vita 1979, Bell 1985, Cohen and Shmida 1993, Bernays and Chapman 1994, Dafni et al. 1997). In addition, spiders can also use floral structures for hiding and for finding sexual partners (Morse and Fritz 1982, Figueira and Vasconcellos-Neto 1992, Morse 1993, Nentwig 1993).

Members of the spider families Thomisidae, Clubionidae, Araneidae, Salticidae, Anyphaenidae, Oxyopidae, Pisauridae, Theridiidae, and Theridiosomatidae were recorded on flowers (Morse 1981, Nentwig 1993, Johnson 1995). Spider family, composition or structure, changes according to foraging strategies and specific requirements (Hatley and MacMahon 1980, Nyffeler et al. 1994, Foelix 1997). However, differences of spider family structure on distinct inflorescence types could also result from other characteristics such as inflorescence architecture and form and colour of flowers.

Flower size has been considered as a main factor explaining significantly different spider assemblages on inflorescences of the plants Lantana camara (Verbenaceae) and Palicourea guianensis (Rubiaceae), in Panama (Nentwig 1993). Thus, flower size should influence spider size distribution through (1) refuge availability, since spiders are frequently preyed upon by birds, and larger spiders seem to be more vulnerable to bird predation (Askenmo 1977, Gunnarsson 1983, 1996), and (2) prey availability, as larger insects are usually attracted to larger flowers (Cohen and Shmida 1993), and only larger spiders can capture large prey (Nyffeler et al. 1994, Carter and Rypstra 1995). Larger flowers should support spiders that can capture larger insects, and consequently should influence the size distribution of visiting spiders. Thus, we tested whether different types of inflorescences are associated with different spider assemblages, and whether body size distribution differs between inflorescences with large vs. small flowers.

MATERIALS AND METHODS

This study was undertaken between March 1997 and February 1999 at Reserva Ecológica do Panga, southeastern Brazil, and include Cerrado–like savannah, old fields, and forest (Schiavini and Araújo 1989). The area is located 40km south of Uberlândia at an average altitude of 800m. All plants used in the experiments were sampled from an old field, dominated by herbaceous plants and small shrubs (< 2m).

Spiders were sampled from 60 inflorescences of 30 individual plants (two inflorescences per individual), of 14 plant species (see Table 1). Branches were carefully enclosed in plastic bags and cut at about 10cm below the inflorescence basal region. These bags were filled with CO_2 to immobilise the spiders before they were counted and fixed with 70% ethanol. The families recorded on all inflorescences were evaluated apart except the web-building spiders that were grouped.

To evaluate the influence of inflorescence characteristics on the abundance of spiders, ten inflorescences, one inflorescence of each plant, from different individuals of each plant species were collected and the following variables recorded:

A. Size (IS), calculated using the formula for the volume of an ellipsoid from the linear inflorescence length from the base to the apex (l), and major the semi-axis of the width (w): $IS = 4/3(\pi l w^2)$ (see Hatley and MacMahon 1980).

B. Colour, classified as yellow, white or blue. All individual inflorescences had only one colour except for Banisteriopsis campestris and Mimosa sp. which were light pink and white, and for simplicity were considered white.

C. Number of flowers: included number of buds, open (nectar-secreting flowers), and senescent flowers.

D. Number of open flowers in each inflorescence (only the nectar-secreting flowers).

E. Flower size, calculated using the formula for the volume of a cone using the diameter (d) and the height (h): $FS = [\pi h(d/2)^2]/3$.

Colour and form effects

To evaluate the effects of colour and form, a factorial experimental design (4 x 2) was carried out between March and April 1998. Only one plant species was used in order to isolate other possible effects of insect attraction or branch architecture among different plant species. Inflorescence models made of cloth, plastic and wire were attached with fine wire to vegetative branches of <u>Baccharis</u> <u>dracunculifolia</u> on four sites distant at least 100 m from each other. The treatment set-up consisted of the most common colours found in natural inflorescences in the field: yellow, white, and blue; green models were also used as controls. Inflorescence forms were umbels and spikes. All inflorescence models had 24 flowers of 2.3cm of diameter, with five separated petals. For each treatment combination, eight inflorescence models were placed on different plants and kept in the field for a week. After this time we collected the inflorescence models in the same way done for natural inflorescences. This procedure was repeated in all four sites.

Flower size effect

Natural inflorescences of <u>B</u>. <u>dracunculifolia</u> (N = 70), <u>M</u>. <u>helvola</u> (N = 30) , <u>D</u>. <u>virgatus</u> (N = 145), and <u>B</u>. <u>gardneri</u> (N = 110) were sampled to test the effect of flower size on the size distribution of flower-dwelling spiders. The diameter of ten randomly chosen open flowers was previously measured and compared with one-way ANOVA followed by Tukey's HSD test, to verify that the plant species had different flower sizes.

The effect of flower size on the size distribution of colonising spiders was also tested, using a randomised experimental block design with spike yellow inflorescence models with 15.0cm height and 24 secondary branches. Two treatments were done to isolate the effects of inflorescence biomass and number of flowers: in the first treatment (small flowers), a 2.3 cm diameter artificial flower was fixed on each secondary branch comprising an inflorescence with 24 flowers; in the second treatment (large flowers), six flowers with 4.6 cm diameter were disposed in alternate secondary branches; the remaining ones had no flowers, but were retained to keep constant number of ramifications and the total flower surface area. This procedure was carried out at three sites. Eight models of each treatment were attached to B. dracunculifolia branches, one model per plant, on each site, left for a week and collected in plastic bags. Eight vegetative control branches were also collected at each site.

Data analysis

Multiple regression analysis was used to evaluate the effects of continuous variables on total spider abundance in natural inflorescences. Multicollinearity was tested among variables before the analysis. The variables that did not contribute significantly to the model were removed through the forward-stepwise method. All analyses used the mean values for each plant species to assess normality of data. Due to the low frequency of web–builder families (web–builders represented 5.7% of all individuals recorded on the natural inflorescences), and the similarities of their foraging strategies, we pooled them into only one group. To evaluate the frequency distribution of families on the inflorescences of the 14 plant species, Canonical Correspondence Analysis was used to relate the distribution of different spider families and environmental characteristics (see Ter Braak 1986). Colour (categorical variable) was including as dummy variable. The environmental matrix was made from the $\log_{10}$-transformed mean values of the characteristics of natural inflorescences. The ordination diagram was constructed based on the first and second canonical axes since they accounted for 84.7% of the variance (see below). Correlations among structural parameters were previously examined to avoid multicollinearity.

The experiments were arranged in four experimental sites randomised as blocks (sites). Analyses of Variance were used to evaluate the results of the experiments, followed by Tukey's HSD multiple comparisons test. Mean spider abundance of all models from each treatment combination used within each block was used in the analysis. Data were $\log_{10}$-transformed for normality, and the homogeneity of variances was checked graphically by plotting residuals against the expected values. The size distribution of spiders was compared using G-test and Kolmogorov-Smirnov test following Sokal and Rohlf (1995).

RESULTS

A total of 581 spiders was recorded in the 14 sampled plant species, the highest spider abundance (17.8%) occurring on inflorescences of Arrabidaea florida (Table 1). Abundance of spiders on inflorescences increased both with flower size and number of open flowers. Abundance was not statistically significantly influenced by number of flowers, although showed a marginal value ($p = 0.075$). Inflorescence size did not contribute to the model, and thus was eliminated by the stepwise method (Table 2).

The most common spider families were Salticidae (32.8%), Thomisidae (30.7%), and Anyphaenidae (22.7%), whereas all web-building spiders comprised only 5.8% of the total. The environmental variables were sufficient to explain the major variation among the spider families (84.8 % on the first two canonical axes). On the ordination diagram, the first axis clearly separated salticids from the other spiders groups, and was positively correlated with total number of flowers, inflorescence size, and flower size (Figure 1). Salticids were found mostly on inflorescences with higher number of flower (Figure 1). The second axis separated thomisids from anyphaenids, miturgids and oxyopids. Thomisids were the most common on inflorescences with larger flowers, whereas anyphaenids, miturgids, and oxyopids were more abundant on larger inflorescences, mainly those with many open flowers. The second axis also separated yellow from blue inflorescences (Figure 1).

Colour and form effects

Inflorescence form did not influence the total number of colonising spiders, but there was a significant effect of colour. Yellow and blue flowers attracted significantly more spiders than the green ones, whereas white flowers were did not differ from the other colours (Table 3).

Guild composition differed among treatments. The interaction of colour vs form had significant effect only on Anyphaenidae (Table 4). Conversely, inflorescence form was not significant for thomisids, and only colour effects influenced their abundance: yellow, white, and blue inflorescences differed from the green ones (Figure 2). On the other hand, only inflorescence form influenced the abundance of miturgids. The umbel models attracted more miturgids than the spike ones (Table 4, Figure 2). Colour and type effects did not influence the abundance of salticids and oxyopids; the latter occurred in very low numbers (Figure 2).

Size distribution of spiders and flower size

The interaction between spider size distribution and flower size was significant ($G_{15} = 44.05$, $\underline{P} < 0.001$). Spiders on inflorescences with small flowers (B. dracunculifolia) differed in size from spiders on inflorescences with larger flowers (D. virgatus and B. gardneri). The size distribution of spiders on M. helvola, which had an intermediate flower size, was not significantly different from the other plant species (Table 5, Figure 3).

A total of 58 spiders were recorded on inflorescence models, 29 on large flowers and 29 on small flower inflorescences. The size distributions were different ($KS = 0.414$, $\underline{P} = 0.011$), with larger spiders more attracted to inflorescence models with larger flowers (Figure 4).

DISCUSSION

Structural complexity, described as the number of leaves per branch, has been considered the main factor influencing the abundance of plant-dwelling spiders on vegetative branches, by enhancing the availability of refuge sites and by reducing the chances of encounters with predators (e.g. Hatley and MacMahon 1980,Gunnarsson 1990). However, on inflorescences, the number of flowers had no influence on spider abundance when flower size and number of open flowers were included in the model. Thus, these two factors were more important for spider abundance than the number of flowers in inflorescences. Although we did not estimate the number of potential prey attracted to inflorescences of different plant species, several studies showed that larger flowers and more open flowers attracted more insects (e.g. Bell 1985, Morse 1986, Cohen and Shmida 1993, Dafni et al. 1997). High density of prey can increase the chances of prey capture success and reduce the variance on prey availability. The inflorescences with characteristics that normally attract more insects can also attract a large number of spiders, but the mechanisms used by spiders for patch location are still obscure.

The distribution of spider families among plant species indicates that spider groups respond differently to inflorescence structural variables. Salticids were most abundant on inflorescences with greater number of flowers, whereas the abundance of thomisids was mainly related to flower size and to yellow flowers. The number of open flowers was insufficient to separate the spider groups, even though it had a strong influence on total spider abundance. On the other hand, inflorescence size did not contribute to explain the total spider abundance, but was important to separate the distribution of abundant families, such as oxyopids, miturgids, and anyphaenids. Inflorescence colours were correlated only with the second ordination axis, but their effects are confounded by other structural variables. However, when experimentally isolated from these variables, the colour affected the total spider abundance. Yellow and blue can attract more insects than white and green, and insect long-distance attraction may involve vision, smell, or both (see Bernays and Chapman 1994). Morse and Fritz (1982) showed that Misumena vatia (Thomisidae) choose branches with greater prey availability at long distances (beyond 1m), where the perception of prey vibration is weak. They proposed that these spiders could reach those sites simply by moving frequently until they find a satisfactory site. Colour and smell are less important for M. vatia, when compared to vibrations stimuli that propagate from the prey through the substrate (Morse 1988). However, his study compared inflorescences within the same plant species, the common milkweed Asclepias syriaca. The inflorescences are regarded as an advertising unit, and their function as a flower aggregation is to enhance the adversiting area to pollinator insects, and consequently the distance that the plant can attract them (Dafni et al. 1997). The visual ability of some spider groups such as wandering spiders is well developed and they may distinguish form, and shade/light contrasts (Foelix 1996). Thus, the advertising unit used by plants to attract insects could also constitute an attractive cue for some spider groups. Spiders have well developed perception systems to detect insect vibrations that propagate through the substrate, but they could also use some cues similar to those used by the insects to detect a satisfactory patch when the vibrations caused by prey are not available. Greco and Kevan (1994) demonstrated that even without any available prey, M.vatia was attracted to yellow colour and to a specific plant species, and proposed that these spiders use vision to select microhabitats. Colour preference was also demonstrated for some Salticidae and Theridiidae species (Foelix 1997, Greco and Kevan 1999). Other spider species could use colour or other inflorescence characteristics to locate adequate patches, as they must have developed a more precise patch choice ability, due to high costs of movement on vegetation (Greco and Kevan 1994, Greco et al. 1995). Our results corroborate these hypotheses, since the spiders were more attracted to some types of inflorescence than others, and mainly because different characteristics of the inflorescences attracted spiders from different families.

When colour and form effects were experimentally separated, colour had a significant effect only on Anyphaenidae and Thomisidae, whereas miturgids responded only to differences in form. Anyphaenids were more abundant on yellow and blue inflorescence models. Thomisids did not discriminate inflorescences of different colours (yellow, white and blue) used in the experiments occurring more abundantly on these inflorescences than on green ones. On the other hand, neither colour nor form differences were significant for salticids and oxyopids. Louda (1982) demonstrated that Peucetia viridans (Oxyopidae) was more attracted by flat-topped inflorescences than vertical ones, suggesting that inflorescence morphology could influence prey availability. She also argued that it should provide some unknown favourable characteristics for those spiders. In our study, oxyopids occurred in low frequencies both on natural and model inflorescences. Previous observations showed that this group is similarly attracted both to natural and to model inflorescences, and to vegetative branches (see chapter 3). The effects of colour and form were not significant for salticids, and agreed with the results from the canonical correspondence analysis, where the abundance of this family had a strong correlation only with the number of flowers (Figure 1). Thus, this study showed that different inflorescence characteristics can attract distinct groups and sizes of spiders. Inflorescence architecture may have more influence than prey abundance for some spider groups, but the opposite can occur for other ones. Alternatively, different inflorescences could attract different insect types or sizes, and consequently spider from distinct families (see Bernays and Chapman 1994). Although most spiders have been regarded as generalists, spider from different families consume insects of different orders in different proportions, and have different degrees of feeding specialisation (Turnbull 1973, Riechert and Luczak 1982, Uetz 1992, Nyffeler et al 1994).

Larger spiders occurred mainly on inflorescences with large flowers when compared to the smaller ones both on empirical and experimental trials. Although we did not measure prey size on large flowers, larger insects may be more frequently attracted by large flowers (see Dafni et al. 1997). Large insects may not be accessible to small spiders, and the vibration from these insects may attract larger spiders. An alternative hypothesis is that large flowers are better hiding places for large spiders. Studies on vegetative branches showed that large spiders are more vulnerable to bird predation, and structural features of the vegetation can influence the microhabitat choice (Waldorf 1976, Askenmo et al. 1977, Gunarsson 1990, 1996)

The differences found in size distribution of spiders and in family structure on different types of inflorescences indicate that specific structural characteristics may result in a typical spider fauna associated with them. It is plausible to suppose that cost/benefit relationships for the plants caused by the presence of these predators on inflorescences can be dependent on the spider assemblage attracted to them. Families with different diet or capture strategies or spiders with different body sizes could influence the production of viable seeds, depending on the proportion of pollinators and captured flower-feeding insects. In fact, positive, negative or negligible effects on the plants due to the presence of different spider species have already been observed (e.g. Morse 1981, Louda 1982, Ott et al. 1998). Studies of the diet of these families on plants and of behaviour involved in patch choice by the different flower-dwelling spider families are critical to predict their possible influences on different plant species.

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Table 1 – Number of spiders recorded on 60 inflorescences of 14 plant species. AN = Anyphaenidae, MI = Miturgidae, OX = Oxyopidae, TO = Thomisidae, SA = Salticidae, WEB = mixed web-builders (Araneidae, Theridiidae, Dictinidae and Scytodidae).

Plant species	AN	MI	OX	TO	SA	WEB	Others	Total
Asteraceae								
Baccharis dracunculifolia	20	3	13	28	11	7	2	84
Bidens gardneri	10	0	3	40	9	6	1	69
Chromolaena laevigata	4	0	1	14	16	0	1	36
Trichogonia melissaefolia	3	0	0	2	5	0	0	10
Bignoniaceae								
Arrabidaea florida	25	5	0	39	32	1	1	103
Lythraceae								
Diplusodon virgatus	22	1	4	7	9	6	0	49
Malpighiaceae								
Banisteriopsis campestris	7	0	2	5	11	2	0	27
Byrsonima intermedia	6	0	0	1	6	0	0	13
Melastomataceae								
Miconia chamissois	3	0	3	9	13	6	0	34
Microlicia helvola	12	7	2	17	7	2	1	48
Mimosaceae								
Mimosa sp	1	0	2	4	0	0	0	7
Rubiaceae								
Palicourea rigida	4	0	0	16	3	0	0	23
Sapindaceae								
Serjania erecta	3	0	0	6	26	2	0	37
Vochysiaceae								
Vochysia tucanorum	10	0	1	27	1	1	1	41
Total	130	16	31	176	188	33	7	581

Table 2 – Multiple regression of the stepwise analysis between the abundance of spiders and total number of flowers, flower size, flowers opened, and inflorescence size. Inflorescence size was not significant and was eliminated by the stepwise method. $R^2 = 0.72$.

Effect	Coefficient	Std Error	F	P
Number of flowers	0.082	0.041	3.963	0.075
Flower size	10.560	3.219	10.760	0.008
Flowers opened	0.416	0.125	11.123	0.008

Table 3 – Analysis of Variance for inflorescence models on number of colonising spiders in four sites (blocks), and HSD Tukey's results with the mean number ± SD of spiders per inflorescence models. Superscripts represent different mean values.

Source	df	Mean–Square	F	P
Site (block)	3	0.049		
Form	1	0.002	0.038	0.846
Colour	3	0.323	5.017	0.009
Form vs. Colour	3	0.012	0.191	0.901
Error	21	0.064		

Results of Tukey comparisons

Yellow	White	Blue	Green
1.38 ± 0.37^{a}	$0.89 \pm 0.56^{a,b}$	1.38 ± 0.46^{a}	0.92 ± 0.29^{b}

Table 4 – Analysis of Variance for form and colour of inflorescence models on numbers of different families that colonised inflorescence models in four sites (blocks).

Source	df	MS	F	P
Anyphaenidae				
Form	1	0.016	0.849	0.367
Colour	3	0.155	8.148	0.001
Form vs. colour	3	0.061	3.181	0.045
Miturgidae				
Form	1	0.049	4.668	0.042
Colour	3	0.005	0.456	0.716
Form vs. colour	3	0.018	1.742	0.189
Oxyopidae				
Form	1	0.019	1.976	0.174
Colour	3	0.012	0.492	0.692
Form vs. colour	3	0.006	0.949	0.435
Salticidae				
Form	1	0.043	0.738	0.701
Colour	3	0.362	0.151	0.309
Form vs. colour	3	0.365	1.273	0.305
Thomisidae				
Form	1	0.001	0.105	0.750
Colour	3	0.040	3.231	0.043
Form vs. colour	3	0.008	0.614	0.614

Legends of Figures

Figure 1 – The distribution of spider families on inflorescences from 14 plant species: Canonical Correspondence Analysis ordination diagram with spider families (•), inflorescence colour centroids (✳) and inflorescence structural parameters (arrows); the first axis is horizontal, second axis vertical. The spider families are Salticidae (SA), Thomisidae (TO), Miturgidae (CL), Oxyopidae (OX), Anyphaenidae (AN), and web-builders spiders (WEB).

Figure 2 – Number of spiders per inflorescence models on different colours of inflorescences. Solid and hatched bars represent spike and umbel models, respectively. Values are means and standard error.

Figure 3 – Spider size distribution on natural inflorescences of four plant species with different flower sizes. The number in parenthesis represents the mean diameter (± SD) of flowers. All plant species had significantly different flower diameters from each other at $\underline{P} < 0.001$ (HSD Tukey's test).

Figure 4 – Spider size distribution on large and small flowers of inflorescence models placed on vegetative branches of B. dracunculifolia.

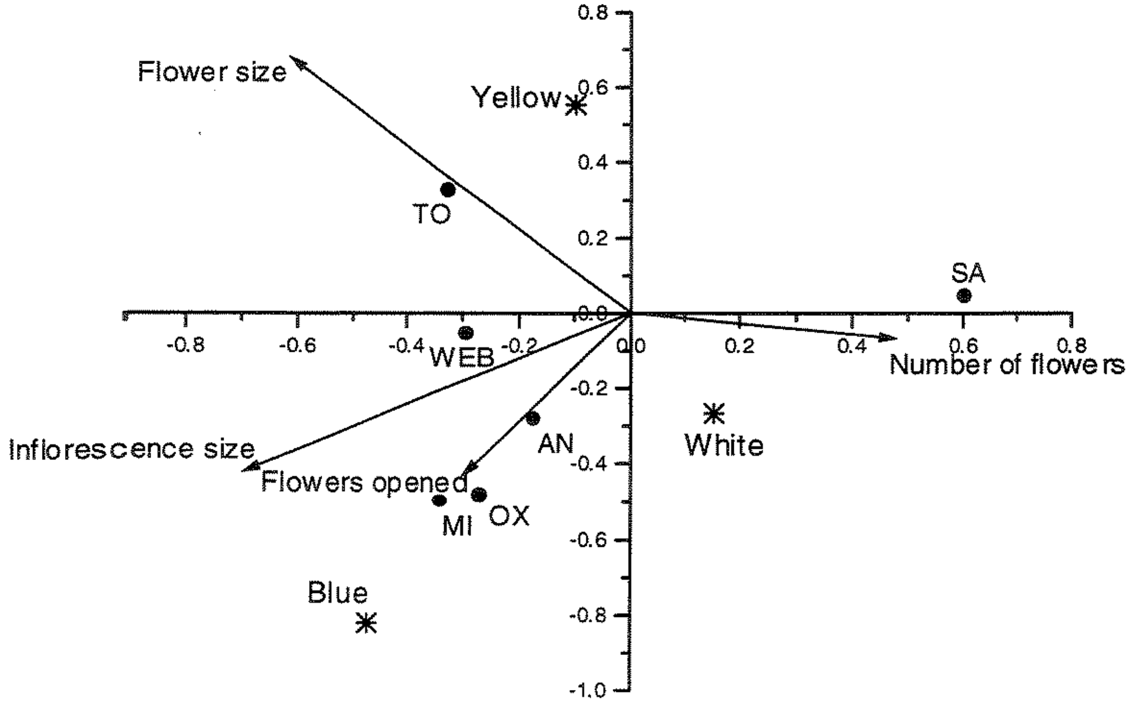
Flower size
Yellow
TO
SA
WEB
Number of flowers
AN
White
Inflorescence size
Flowers opened
MI
OX
Blue
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8

Figure 1

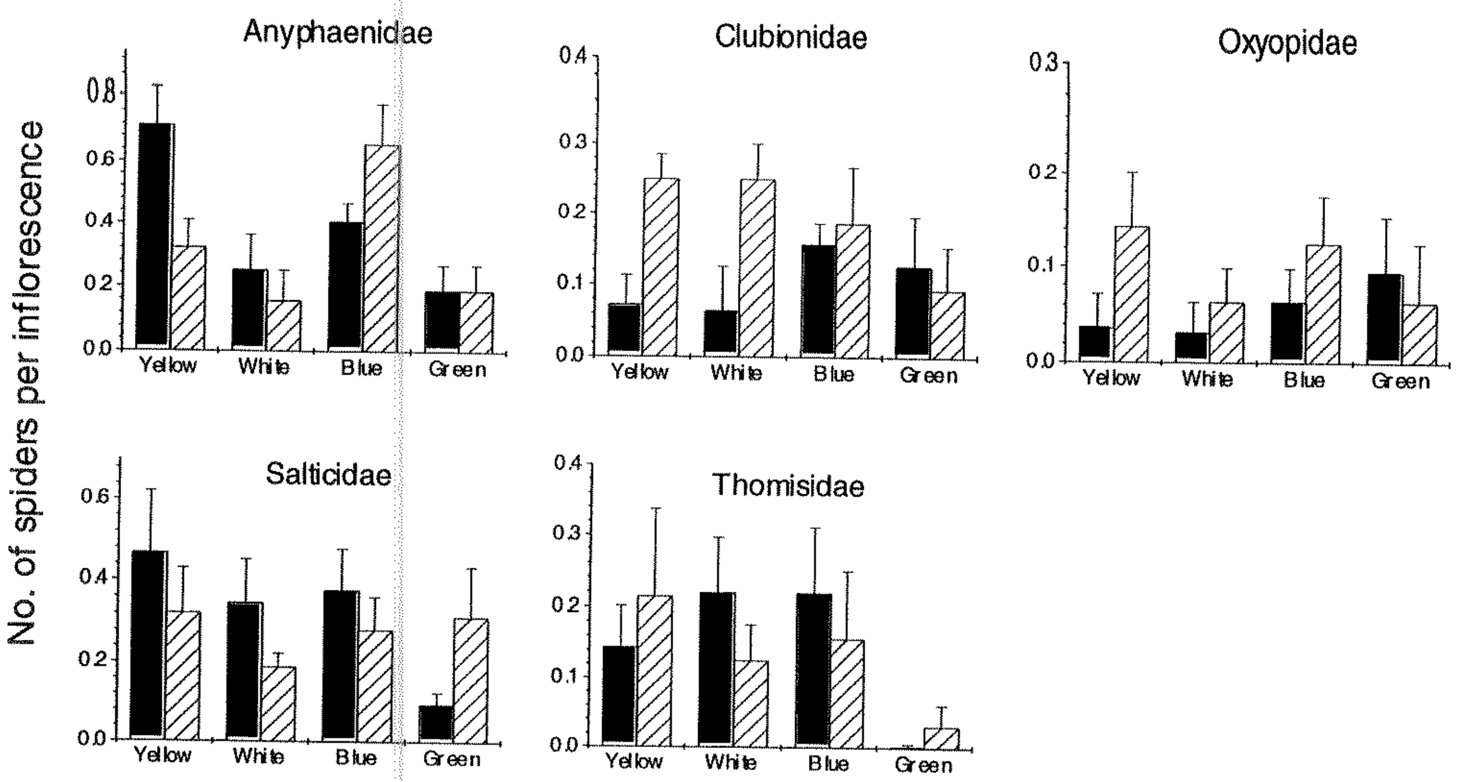
Anyphaenidae
Clubionidae
Oxyopidae
Salticidae
Thomisidae
No. of spiders per inflorescence
0.0
0.2
0.4
0.6
0.8
0.1
0.3
Yellow
White
Blue
Green

Figure 2

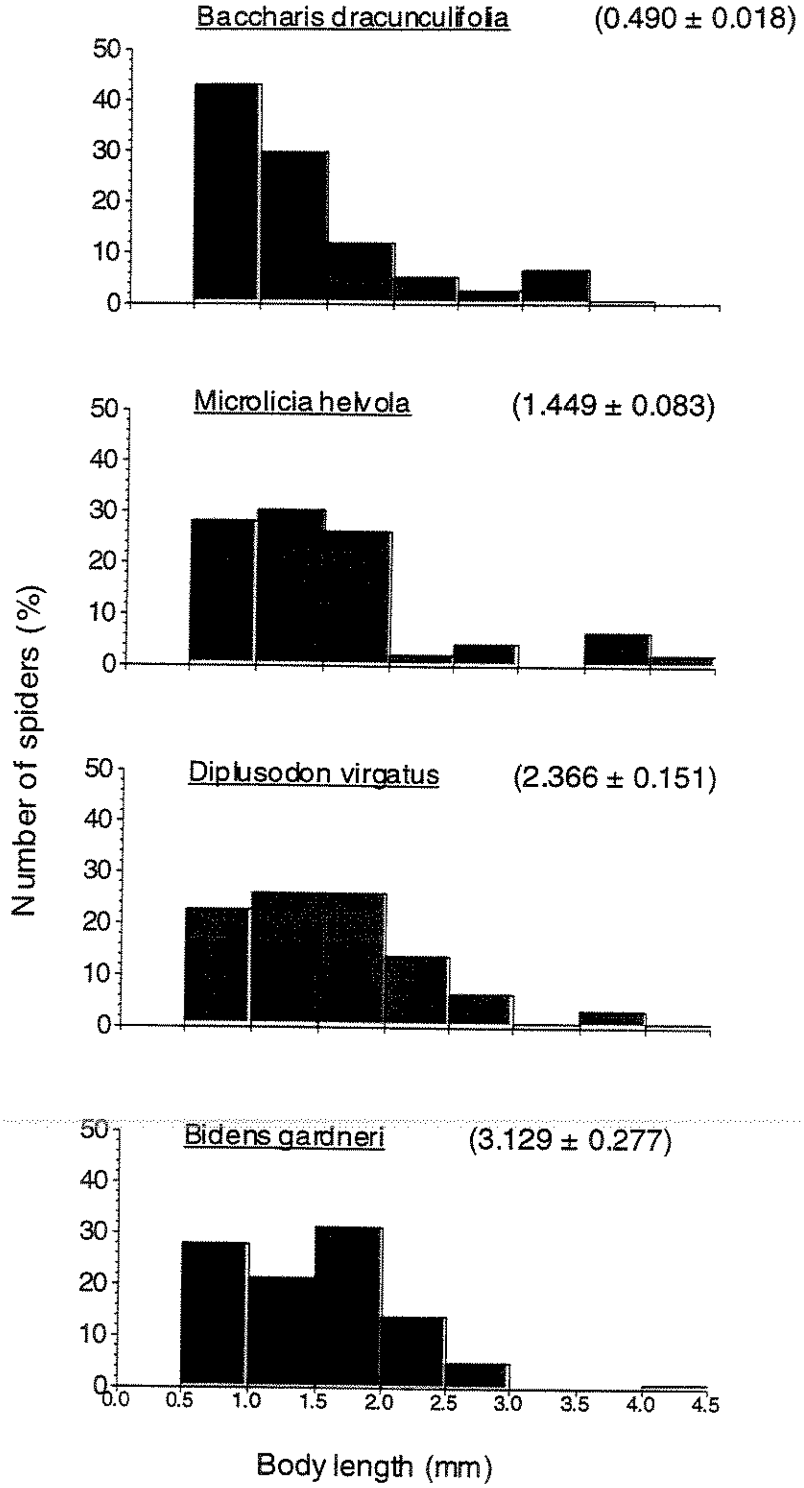
Baccharis dracunculifolia
(0.490 ± 0.018)
Microlicia helvola
(1.449 ± 0.083)
Diplusodon virgatus
(2.366 ± 0.151)
Bidens gardneri
(3.129 ± 0.277)
Number of spiders (%)
0
10
20
30
40
50
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
Body length (mm)

Figura 3

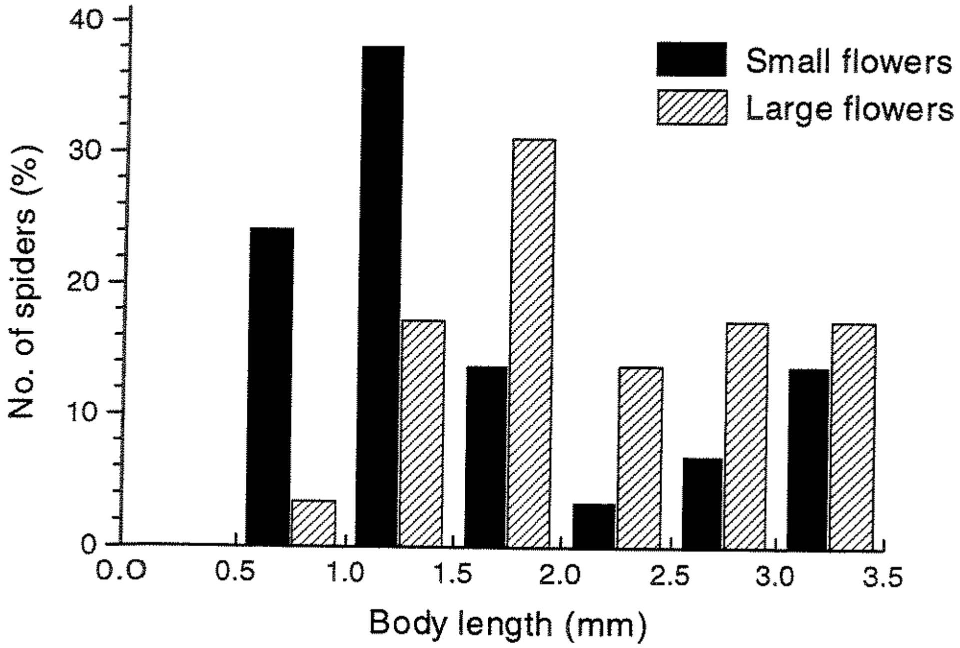
40
30
20
10
0
No. of spiders (%)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
Body length (mm)
Small flowers
Large flowers

Figura 4

CAPÍTULO 5

CONSIDERAÇÕES FINAIS

COMPLEXIDADE ESTRUTURAL DE PLANTAS

Este estudo mostrou que a complexidade estrutural das plantas, descrita como o número de folhas e corrigida pelo volume do ramo, foi o principal fator que influenciou a densidade de aranhas entre espécies de plantas arbustivas. A distribuição das famílias de aranhas diferiu entre Baccharis dracunculifolia, Diplusodon virgatus e Bidens gardneri. Oxyopidae e Salticidae ocorreram com maior frequência em espécies de plantas com maior densidade de folhas. No entanto, a frequência de Oxyopidae não diferiu entre ramos vegetativos e inflorescências, enquanto Salticidae foi mais abundante em inflorescências do que em ramos vegetativos. Espécies pertencentes a estas duas famílias tem sido consideradas como membros de uma mesma guilda, devido à semelhanças na acuidade visual, no comportamento de captura de presas, e na proporção de outras aranhas em sua dieta (e.g. Hatley and Mac Mahon 1980, Nyffeler et al. 1994, Halaj et al. 1997). No entanto, os resultados deste estudo mostraram que estas famílias podem diferir em escolha de microhabitat.

A abundância de presas (Hurd e Fagan 1992, Nentwig 1993), a disponibilidade de refúgios contra predadores (Askenmo et al. 1977, Gunnarsson 1990, 1996) e condições físicas ambientais (Evans 1997, Henschell e Lubin 1997), tem sido propostas como os principais fatores que influenciam a distribuição de aranhas. Condições físicas do ambiente como umidade precipitação e temperatura podem limitar populações de aranhas em substratos que possuem poucos locais de refúgio (p.ex.Henschell e Lubin 1997). A disponibilidade de locais de refúgio pode também determinar a abundância de espécies de aranhas que são vulneráveis a eventos de predação por aves (Askenmo et. al. 1977, Gunnarsson 1996) ou por outras aranhas (Polis et al. 1989, Wise 1993). No entanto, em plantas, fatores como disponibilidade de presas e de refúgios estão normalmente confundidos. Algumas das espécies abundantes nos ramos vegetativos de B. dracunculifolia, D. virgatus e B. gardneri analisadas neste estudo, possuem uma ampla distribuição. Por exemplo, Cheiracanthium inclusum (Miturgidae), Oxyopes salticus (Oxyopidae), Misumenops pallens e M. pallida (Thomisidae) são abundantes em várias regiões brasileiras e em algumas regiões da America do Norte (see Hatley and MacMahon 1980, Santos e Brescovit comum. pess.). Estas espécies de ampla distribuição estão presentes, em vários tipos de habitats e devem utilizar várias espécies de plantas como substrato. Estudos posteriores poderiam avaliar se o efeito da complexidade estrutural de plantas na abundância de espécies de aranhas que possuem ampla distribuição varia entre regiões. A estrutura do microhabitat pode ser mais importante para a sobrevivência de algumas espécies em determinadas regiões do que a abundância de presas devido à condições físicas extremas ou devido a presença de predadores visualmente orientados como aves e vespas.

ARANHAS QUE HABITAM FLORES

A abundância de aranhas foi maior em inflorescências naturais do que em ramos vegetativos, nas quatro espécies de plantas analisadas. Uma grande quantidade de insetos são atraídos por flores (Bernays e Chapman 1994), mas a estrutura física das inflorescências parece propiciar sítios favoráveis para estes predadores, ou pelo menos para parte deles, uma vez que inflorescências artificiais dispostas em B. dracunculifolia também atraíram um maior número de aranhas do que os ramos vegetativos desta mesma espécie. Salticidae, Miturgidae e Anyphaenidae ocorreram preferencialmente em inflorescências artificiais quando comparadas com ramos vegetativos. Apesar de que diferenças na disponibilidade de presas entre inflorescências naturais e artificiais não ter sido estimada, as inflorescências artificiais devem atrair uma menor quantidade de insetos, uma vez estas não possuem características como odor e textura que são fatores importantes para a atração de muitos insetos. Além disto, a abundância de presas pode não ser o fator limitante para algumas espécies (veja Wise 1993, Foelix 1996, Henschell and Lubin 1997). Assim, disponibilidade de refúgios contra predadores pode ter sido a principal causa na determinação da escolha destes locais para os membros destas famílias. Por outro lado, Oxyopidae, Thomisidae e aranhas construtoras de teia não diferiram entre os dois tipos de ramos. Thomisidae foi a única família que ocorreu apenas na época de floração de B. dracunculifolia. e parecem estar mais associados às inflorescências naturais e não responder apenas às características estruturais das inflorescências. Assim, as características que diferem entre os dois tipos de inflorescências podem constituir fatores fundamentais para a atração de Thomisidae por inflorescências. Por exemplo, recentemente, alguns autores demonstraram que algumas espécies do gênero Xysticus e Misumena vatia (Thomisidae) podem ser atraídas por compostos químicos (Aldrich and Barros 1995, Krell and Krämer 1998). Morse & Fritz (1982) observaram que Missumena vatia (Thomisidae) usualmente caçam em flores de alta qualidade, que atraem um maior número de insetos. Assim, é possível que diferentes famílias de aranhas possam utilizar diferentes espécies de planta ou partes de uma mesma planta ajustando às suas necessidades específicas e a disponibilidade de refúgios ou de presas podem determinar as diferenças na distribuição de famílias de aranhas.

Dentre as inflorescências naturais das 14 espécies de plantas analisadas, o tamanho da flor (expresso através de seu diâmetro) e o número de flores abertas foram as variáveis mais importantes na determinação da abundância de aranhas, mas as famílias analisadas neste estudo responderam diferencialmente à variáveis como o tamanho da inflorescência, sua complexidade estrutural, forma e cor. No entanto, os mecanismos usados por aranhas de diferentes famílias para encontrar estas inflorescências ainda permanecem obscuros. O comportamento de escolha de habitat de aranhas que vivem em plantas parece ser complexo, pois além das características estruturais do microhabitat, as interações entre estes predadores também devem ser importantes na decisão de escolha. A predação entre aranhas de diferentes tamanhos parece ser frequente (Uetz 1977, Polis et al. 1989, Wise 1993), mas diferenças nas táticas de captura de presas podem influenciar os resultados destas interações (Ehmann e MacMahon 1996). Características inerentes às espécies pertencentes a diferentes famílias como tamanho, agilidade, acuidade visual e comportamento de captura de presas podem determinar os resultados de interações entre membros de famílias diferentes que co-ocorrem num dado microhabitat. A relação entre as características da arquitetura das inflorescências e a ocorrência das famílias nestes habitats podem estar sendo influenciadas por interações entre estes predadores, o que poderia obscurecer os atributos usados pelas aranhas na escolha de inflorescências.

As aranhas são consideradas predadores generalistas, mas podem possuir diferentes graus de especialização de presas com relação à composição taxonômica e ao tamanho dos insetos consumidos (Turnbull 1973, Riechert e Luczak 1982, Nyffeler e Sterling 1994, Foelix 1996). Estas diferenças podem depender da morfologia (incluindo tamanho, sexo e idade), disponibilidade da presa, táticas de captura, condições climáticas e do substrato de forrageamento (Turnbull 1973, LeSar e Unzicker 1978, Riechert e Luczak 1982, Nyffeler et al. 1994). No entanto, os trabalhos que enfocam a influência de insetos polinizadores ou dos que causam danos em flores, raramente mencionam a presença de artrópodes predadores e seus efeitos no sucesso reprodutivo das plantas. Louda (1982) mostrou que Peucetia viridans (Oxyopidae) é abundante nas inflorescências de Haplopappus venetus (Asteraceae) e que podem provocar uma redução no número total de sementes produzidos por esta espécie de planta, mas a presença destes predadores levaram a um aumento no número de sementes viáveis produzidas, através de interações entre as aranhas e os insetos polinizadores e outros insetos herbívoros que causam danos às flores e sementes. Por outro lado, Ott et al. (1998) demonstraram que o thomisídeo Misumenops celer altera a morfologia das flores de Phox roemeriana (Polemoniaceae) e consequentemente diminui a produção de sementes. Caso estes fenômenos sejam frequentes em sistemas naturais, as aranhas devem influenciar a dinâmica populacional de plantas entomófilas, ou as que têm suas flores atacadas por insetos herbívoros. O efeito da presença destes predadores na produção de sementes viáveis deve depender da abundância, do tamanho, e da estratégia de captura de presas das aranhas que visitam as inflorescências. Este estudo mostrou que variáveis como tamanho, complexidade estrutural das inflorescências, bem como o número, tamanho e cor de flores podem determinar a abundância total, a composição e a frequência relativa de famílias além da distribuição de tamanhos de aranhas que visitam estas inflorescências. Como as espécies que compõem estas famílias adotam diferentes estratégias de forrageamento, o impacto causado pela presença destes predadores pode estar indiretamente condicionado às características estruturais das inflorescências. Estudos enfocando o comportamento de escolha de habitat destes predadores e o impacto causado pela presença de diferentes espécies de aranhas em inflorescências, na produção de sementes viáveis, podem esclarecer questões acerca de processos que envolvem insetos polinizadores e outros insetos herbívoros e suas plantas hospedeiras.

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