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Negative effects of ant foraging on spiders in Douglas-fir canopies

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Abstract Spiders and ants are potential competitors and mutual predators. Indirect evidence from previous research has suggested that ant foraging may significantly lower the abundance of arboreal spiders in young Douglas-fir plantations in western Oregon. This study tested the effect of foraging by ants, dominated by *Camponotus* spp., on spider assemblages in Douglas-fir canopies in a 5-month ant-exclusion experiment. The biomass of potential prey organisms on foliage, dominated by Psocoptera, increased significantly by 1.9- to 2.4-fold following ant exclusion. The removal of ants did not affect the abundance of flying arthropods in the vicinity of tree canopies as indicated by sticky trap catches. The abundance of hunting spiders, the majority being Salticidae, increased significantly by 1.5- to 1.8-fold in trees without ants in the late summer; neither the abundance of web-building spiders nor the average body size of hunting and web-building spiders were significantly affected by ant removal. Spider diversity and community structure did not differ significantly between control and ant-removal trees. The majority of prey captured by ants were Aphidoidea (48.1%) and Psocoptera (12.5%); spiders represented only 1.4% of the ants' diet. About 40% of observed ants were tending *Cinara* spp. aphids. Our observations suggest that the lower abundance of hunting spiders in control canopies with ants may be due to interference competition with ants resulting from ant foraging and aphid-tending activities. Direct predation of spiders by ants appeared to be of minor importance in this study system. This study did not provide sufficient evidence for exploitative competition for prey between ants and spiders.

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Introduction

Ants and spiders are among the most ubiquitous and diverse predators in terrestrial ecosystems. Many species share the same trophic level and can potentially compete with and prey upon each other (see review in Wise 1993).

Despite reports of high rates of predation by ants on spiders in some systems (Petal and Breymeyer 1969; Kajak et al. 1972), most observational studies have found no significant differences in spider densities between areas of high and low ant foraging activity (Otto 1965; van der Aart and de Wit 1971; Brüning 1991). As an exception, Cherix and Bourne (1980) reported lower densities of large wolf spiders and a lower spider species richness within a super-colony of *Formica lugubris* Zett. Exclusion experiments in pastures with the imported fire ant, *Solenopsis invicta* Buren, revealed only slight negative effects of ant presence on two species of hunting spiders (Lycosidae and Clubionidae) (Howard and Oliver 1978). A similar experiment conducted in a cotton field in Texas with the same species of fire ant failed to detect any changes in spider densities in ant-removal plots (Sterling et al. 1979). At present, clear experimental evidence on the significance of competition and direct predation between spiders and ants is lacking (Wise 1993).

Spiders and ants are the most abundant predatory arthropods in the canopies of coniferous forests in the northwestern United States (Dahlsten et al. 1977; Campbell et al. 1983; Moldenke et al. 1987; Schowalter 1989; Halaj 1996). Carpenter ants, *Camponotus* spp., which are abundant and widespread foragers in Douglas-fir, *Pseudotsuga menziesii* (Mirbel) Franco, canopies, have been implicated to be important predators of some insect species such as western spruce budworm, *Choristoneura occidentalis* Freeman, and Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough) (Campbell and Torger-

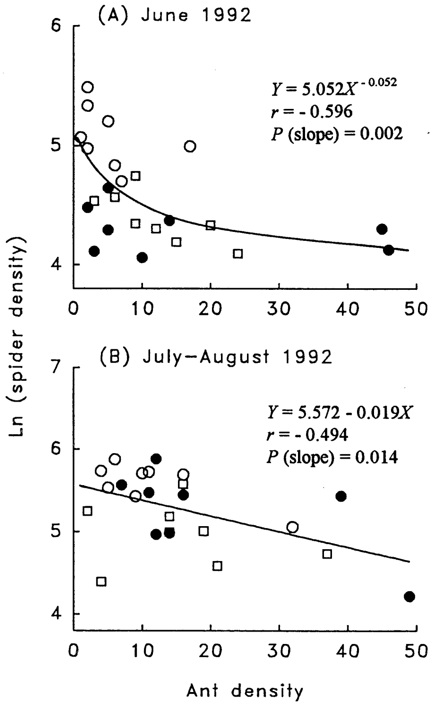

Fig. 1 Relationship between the abundance of spiders and ants in three geographic provinces of western Oregon; ● western Coast Range, ○ eastern Coast Range, □ western Cascade Range. Individual data points represent arthropod densities collected from lower crown branches of 50 sapling Douglas-fir trees (three 45-cm-long branch tips sampled per tree) at one study site. Site descriptions and details on the sampling protocol are reported in Halaj et al. (1996)

sen 1982; Campbell et al. 1983; Mason and Torgersen 1983; Youngs and Campbell 1984). For example, Campbell and Torgersen (1982) estimate 80–90% pupal mortality rates of western spruce budworm, due to ant predation, and postulate that ants may play a prominent role as mortality factors in the population dynamics of this lepidopteran.

During an observational study on the abundance and distribution of arboreal spiders and ants in young Douglas-fir plantations across western Oregon (spider data summarized in Halaj et al. 1996), we noticed significantly lower densities of arboreal spiders at sites with higher densities of foliage-foraging *Camponotus* and *Formica* spp. ants (Fig. 1). The pattern observed in June 1992 (Fig. 1A) was mostly due to a negative correlation between the abundance of web-building spiders and ants in this region ($r = -0.60$, $P = 0.002$). On the other hand, a negative association between densities of hunting spiders and ants ($r = -0.43$, $P = 0.034$) accounted for most of the spider-ant relationship detected in late July/early August 1992 (Fig. 1B). Furthermore, on several occasions, while taking beating samples of foliage, we also observed attacks of dislodged ants (mostly *Camponotus* and *Formica* spp.) on spiders and other arthropods present on the beating sheet (A.R. Moldenke and J. Halaj, personal observation). Thus, accumulated indirect evidence suggests that foraging by ants may represent a negative factor in the biology of arboreal spiders in young Douglas-fir plantations. However, the importance of competition or direct predation between ants and spiders has not been experimentally investigated in this system.

The objective of this study was to determine whether or not exclusion of ants affected spider assemblages in Douglas-fir canopies. In view of the documented impact of foraging by ants on population densities of some insects in Douglas-fir canopies (e.g., Campbell and Torgersen 1982; Campbell et al. 1983), and the observed negative associations between spider and ant densities in western Oregon, we hypothesized that removing ants would have a positive effect on the abundance of spiders in the canopy. In this study, we present direct experimental evidence of a negative effect of ant foraging on the abundance of arboreal hunting spiders in young Douglas-fir plantations. Based on our observations, we suggest that this is due to interference competition between ants and spiders resulting from ant foraging and aphid-tending activities.

Materials and methods

Study area

The study was conducted at the H. J. Andrews Experimental Forest within the Willamette National Forest in the western Cascade Province of Oregon, USA. This province is characterized by wet winters, warm and dry summers, and mild temperatures throughout the year. The annual precipitation is approximately 230 cm, with the majority of precipitation occurring between November and March. Mean annual temperature for the province is 7.9°C (Taylor and Bartlett 1993).

The study site was in a young plantation of Douglas-fir, with occasional western hemlock, *Tsuga heterophylla* (Rafinesque) Sargent, and western redcedar, *Thuja plicata* D. Don., at an elevation of 800 m. The ground vegetation included dense patches of bracken fern, *Pteridium aquilinum* (L.) Kuhn in Decken, *Gaultheria shallon* Pursh, fireweed, *Epilobium angustifolium* L., and Pacific rhododendron, *Rhododendron macrophyllum* D. Don ex G. Don. The site contained large amounts of coarse woody debris, which provided excellent nesting sites for carpenter ants.

Study design

The study had a completely randomized design structure, with two treatments randomly assigned to a total of 30 interdispersed young Douglas-fir trees (<15 years old, <10 m tall). Ants were excluded from 15 trees with 50-cm-wide sticky barriers of Tanglefoot (Tanglefoot, Grand Rapids, Mich.) applied to the base of tree trunks on 15 May 1994 (hereafter referred to as “ant-free” trees). In addition, vegetation (occasional stems of bracken fern and fireweed) touching the lower crown branches of exclusion trees was removed to eliminate “bridges” frequently used by ants to access tree canopies. An equal number of trees ($n = 15$) was left untreated to serve as controls.

Arthropod sampling

Within each tree, 1-m-long tips of three randomly selected branches from the lower third of the canopy were sampled. Branches selected for sampling were permanently marked with a short strip of plastic ribbon. Arthropods were sampled by beating branches with a plastic rod over a hand-held drop cloth. All arthropods dislodged onto the drop cloth were collected with a portable battery-powered vacuum collector (Paul and Mason 1985) and preserved in 75% ethanol. To assess the initial conditions in the study system (Hairston 1989), all trees were sampled on 12 May 1994, before the exclusion of ants. Beginning 6 weeks after the exclusion of ants, trees were sampled five times at 1-month intervals on 28 June, 30 July, 27 August, 24 September and 29 October 1994.

We used a series of sticky traps to assess the impact of ant foraging on the spectrum of flying arthropod prey at the study site. Traps were Tanglefoot-coated sheets (180 × 270 mm) of a clear, rigid plastic mesh with a grid size of 2 × 2 mm. In each tree category (control and ant-free trees), traps were assigned to ten randomly selected trees. Each trap was attached to a wooden stick using two push pins and was positioned vertically at a height of 170 cm above ground, approximately 1 m from the tree canopy. The cardinal direction from the tree at which the trap was positioned and the orientation of the trap were determined randomly. From 30 July 1994, the traps were exposed in the field for 48 h during each monthly foliage sampling period. Due to technical problems, we did not use the traps on earlier sampling dates.

In the laboratory, captured arthropods other than spiders were sorted to order, and spiders were sorted and identified to species when possible. The body length of spiders was measured to the nearest 0.05 mm (excluding chelicerae and spinnerets); the body length of other arthropods was measured to the nearest 0.5 mm. The biomass of all arthropods was estimated with body-length-based regression models in Rogers et al. (1977) and Halaj (1996).

Based on their use of silk to construct webs, spiders were categorized into two basic functional groups: web-building spiders and non-web builders or cursorial hunting spiders. To describe the structure of the spider community in the canopy, the hunting and web-building spiders were further divided into foraging categories based on classifications in Gertsch (1979) and Hatley and MacMahon (1980). Hunting spiders included: (1) agile hunters of the families Salticidae and Oxyopidae, a group of active foragers with keen vision; (2) ambushers of the family Thomisidae; (3) runners of the family Philodromidae, a group of spiders combining active search and ambush strategies; (4) nocturnal hunters including Clubionidae, Anyphaenidae, and Gnaphosidae, spiders which actively search foliage at night. Web-building spiders were divided into categories of spiders with similar web characteristics and included: (1) orb-weavers of the families Araneidae and Tetragnathidae; (2) comb-footed spiders, family Theridiidae; (3) sheet-web weavers of the families Linyphiidae and Erigonidae; (4) hackled-band weavers, family Dictynidae.

Predator foraging and diets

The foraging behavior of predators was observed on the marked branches of all 30 trees at 3- to 4-week intervals between 9 June and 16 October 1994. On each date, between 0800 and 1700 hours, approximately 2 min were spent observing each branch. The species of foraging ants and spiders, their prey organisms, their mutual interactions, and frequencies of aphid tending by ants were recorded. Prey-carrying ants and spiders were collected and preserved in 75% ethanol.

Additional behavioral and dietary data on ants and spiders were collected at the same site at 2- to 3-week intervals between 16 June and 14 September 1995. The foliage and trunks of young Douglas-fir trees selected haphazardly along 100-m-long transects were searched for predators. Data were collected as in 1994. In addition, the composition of the diet of web-building spiders was assessed. All trapped insects and the resident spiders were removed from webs located in the lower third of Douglas-fir canopies and preserved in 75% ethanol.

Due to the low frequency of prey-carrying ants in the canopy in 1994, additional information on the ants' diet was collected by observing them as they entered their nests. Three colonies (built in old tree stumps) of the most common canopy forager, *Camponotus laevigatus* (Smith), were sampled. Workers carrying prey organisms to the nest were collected with an aspirator and preserved in 75% alcohol. Nests were monitored for a total of 14.1 h on ten dates between 4 July and 14 September 1995.

Data analyses

Data obtained from individual branches of each treatment tree were averaged before analyses. Treatments were compared using estimates of arthropod densities per branch. Since the same trees and branches were sampled over time, the data were analyzed with two-way (ant and date effects) repeated-measures ANOVAs. In the case of a significant date by treatment interaction, the effect of ant exclusion was evaluated on individual sampling dates. To control for multiple comparisons, probability levels in simultaneous tests were adjusted with the sequential Bonferroni technique (table-wide α level = 0.05) (Holm 1979; Rice 1989). In order to satisfy the assumption of homogeneous variance in ANOVA, variables were transformed to $\ln(Y)$, $\ln(Y + 1)$, or $\ln(Y + 0.01)$. In all cases, original means and standard errors are reported. Diversity of spider populations was defined by the Shannon diversity index (H') (Pielou 1975). Body-size frequency distributions of arthropods were compared with the Kolmogorov-Smirnov two-sample test. The G-test of independence with the Williams correction was used to determine similarities in taxonomic composition of diets of spiders and ants (Sokal and Rohlf 1995). Taxonomic and body-size overlap between diets of spiders and ants were calculated with the formula in Schoener (1968). All statistical analyses were performed with SAS computer programs (SAS Institute 1985).

Results

Abundance of potential prey

The biomass of arthropod prey on foliage did not differ between the two groups of trees in pretreatment samples ($F = 0.01$, $df = 1{,}27$, $P = 0.911$). Following the exclusion of ants, the biomass of prey in ant-free trees was significantly higher than in the controls (overall mean: $F = 22.98$, $df = 1{,}27$, $P < 0.001$), reaching a 2.4-fold difference between the treatments in late August ($F = 18.56$, $df = 1{,}27$, $P < 0.001$) (Fig. 2A). Differences between the treatments were dependent on sample dates (Wilk's lambda: $F = 9.44$, $df = 4{,}24$, $P < 0.001$). The increase in number of prey was mostly due to an increase in the abundance of barklice, Psocoptera, which were the most common arthropods on foliage, accounting for about 61% and 87% of individuals, and 61% and 67% of prey biomass in control and ant-free trees, respectively. The most abundant psocid species were *Teliapsocus conterminus* (Walsh) and *Caecilius* spp. A significantly higher biomass of arthropods was recorded in control trees in late October ($F = 7.56$, $df = 1{,}27$, $P = 0.011$). This was largely due to a substantial increase in the number of Collembola migrating from the forest litter into the tree canopies. Their low numbers in ant-free trees were likely due to the presence of sticky barriers on tree trunks.

Ant foraging did not have any significant effect on the biomass of flying arthropods in the vicinity of control versus ant-free trees (overall mean: $F = 0.001$, $df = 1{,}18$, $P = 0.96$) (Fig. 2B). The majority of trapped prey were Diptera, accounting for about 72% of the total number, and 67% and 58% of the total biomass of flying insects in the vicinity of control and ant-free trees, respectively.

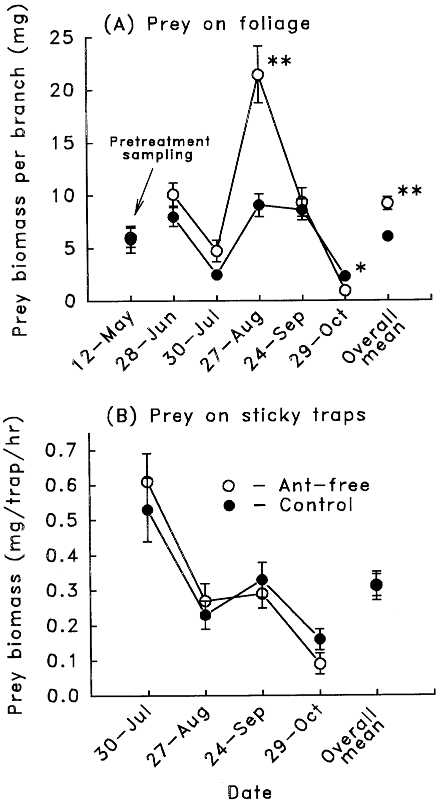

Fig. 2. Biomass of potential insect prey organisms from foliage-beating samples (**A**) and sticky traps (**B**). *Bars* indicate standard errors. Probability levels ($*P < 0.05$, $**P < 0.01$) adjusted for multiple comparisons with the sequential Bonferroni test (number comparisons k = five sampling dates; table-wide α level = 0.05)

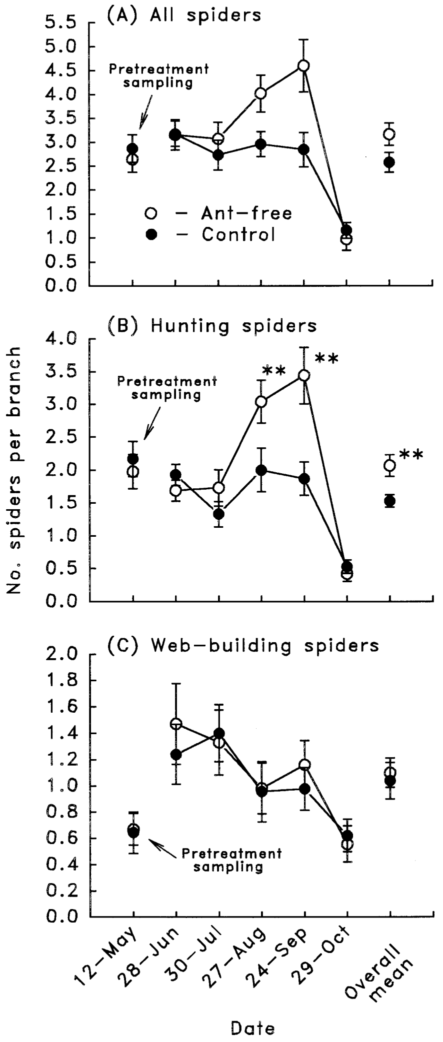

Fig. 3 Number of total spiders (**A**), hunting spiders (**B**) and web-building spiders (**C**) per 1-m-long branch tip as determined from foliage-beating samples. *Bars* indicate standard errors. Probability levels ($**P < 0.01$) adjusted for multiple comparisons with the sequential Bonferroni test (number comparisons k = five sampling dates; table-wide α level = 0.05)

Abundance and diversity of spiders

There were no differences in the total abundance of spiders between the two groups of trees prior to exclusion of ants ($F = 0.30$, $df = 1{,}28$, $P = 0.587$). The same was true when considering separately the abundance of hunting and web-building spiders ($F = 0.26$, $df = 1{,}27$, $P = 0.614$, and $F = 0.01$, $df = 1{,}27$, $P = 0.905$, respectively). Following the exclusion of ants, the total abundance of spiders in ant-free trees increased steadily (Fig. 3A). The ant effect was date dependent (Wilk's lambda: $F = 4.08$, $df = 4{,}112$, $P = 0.008$), with a marginally significant difference (table-wide cut-off $P = 0.010$) recorded only in late September ($F = 7.17$, $df = 1{,}28$, $P = 0.012$) (Fig. 3A). Hunting spiders alone followed a similar trend, reaching a significantly higher abundance in ant-free trees in late August and September ($F = 8.00$, $df = 1{,}28$, $P = 0.009$ and $F = 9.95$, $df = 1{,}28$, $P = 0.004$, respectively) (Fig. 3B). A greater abundance of hunters in ant-free trees reflected mostly increased densities of agile hunters recorded in late August and September ($P = 0.032$ and $P = 0.012$, respectively) and anyphaenids among nocturnal hunters in late September ($P = 0.008$). There was also a slight increase in the abundance of philodromids in ant-free trees in late August ($P = 0.074$). Neither the densities of web-building spiders as a whole (overall mean: $F = 0.10$, $df = 1{,}28$, $P = 0.748$) (Fig. 3C), nor the abundance of individual web-building spider groups were significantly different between treatments on any sample date.

There were no significant differences in spider species richness or diversity between control and ant-free trees on any sample date (Fig. 4). A slightly higher spider species richness and diversity in ant-free trees in late summer reflected the collection of several individuals of "rare species" (in relation to the overall spider abundance in the study) of hunting spiders, such as *Phidippus johnsoni* (G. & E. Peckham), *Misumena vatia* (Clerck), *Misumenops celer* (Hentz), *Xysticus gosiutus* Gertsch and *Sergiolus* sp., in this period.

The exclusion of ants did not have a significant effect on the overall spider community structure. The significant increase in absolute densities of hunters in ant-free

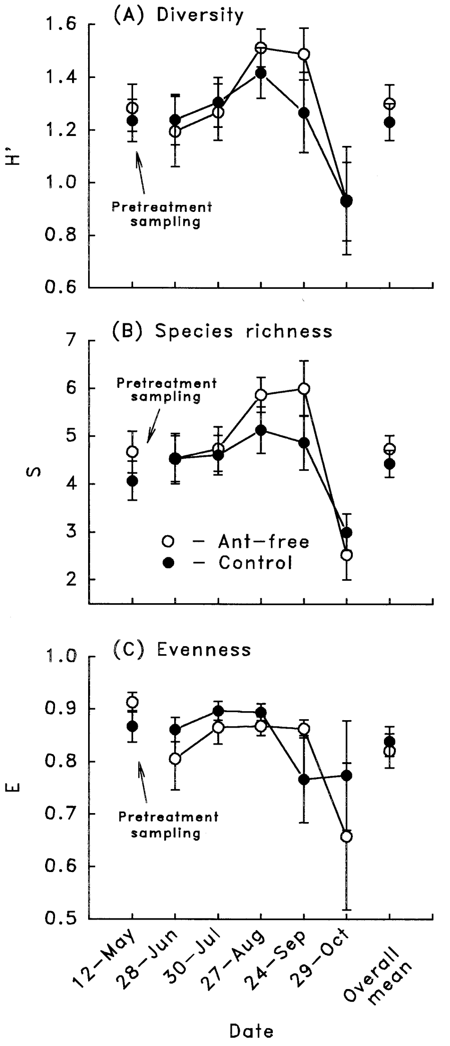

Fig. 4 Diversity (**A**), species richness (**B**) and evenness (**C**) of spiders on Douglas-fir foliage. *Bars* indicate standard errors. No significant differences were detected on any sample date

trees was not strong enough to induce significant changes in the spider community structure. Hunting spiders were the principal group, representing 60% and 64% of all spiders in control and ant-free trees (Fig. 5). This difference was not significant (overall mean: F = 0.803, df = 1,28, P = 0.378). The 1.84-fold increase in the absolute abundance of hunting spiders in ant-free trees in late August resulted in only a slight increase in the relative representation of this group in the overall spider community on this date [i.e., control: 0.68 ± 0.05 (mean ± SE); ant free: 0.74 ± 0.03; F = 1.10, df = 1,28, P = 0.302]. Similarly, no statistical differences were found in proportions of individual spider groups between the two categories of trees. About 70% of hunting spiders were agile hunters. A jumping spider, *Metaphidippus aeneolus* Curtis, accounted for 84% of the abundance of agile hunters. The majority of web-building spiders were sheet-web weavers of the families Linyphiidae and Erigonidae (Fig. 5).

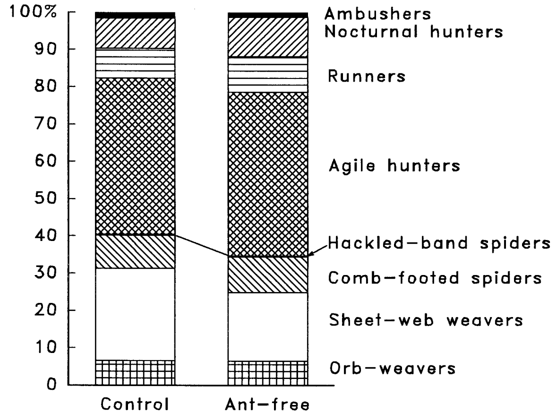

Fig. 5 Relative abundance of spider guilds in control and ant-free canopies. Pooled data from five sample dates

In addition, the exclusion of ants did not have a significant effect on the average body size of total spiders (control: 2.245 ± 0.062; ant free: 2.129 ± 0.050; main effect: F = 2.135, df = 1,28, P = 0.155) and hunting spiders (control: 2.609 ± 0.073; ant free: 2.506 ± 0.059; main effect: F = 1.218, df = 1,28, P = 0.279), and had only a weak negative effect on the average body size of web-building spiders (control: 1.724 ± 0.050; ant free: 1.577 ± 0.060; main effect: F = 3.460, df = 1,28, P = 0.074).

Diet composition of spiders and ants

Out of 723 ants observed in the canopy over the two seasons, only 11 individuals were found carrying prey organisms (Table 1). Only once did we observe an ant feeding on a spider in the tree canopy: a worker of *Camponotus modoc* Wheeler, was observed carrying a fresh body of a male jumping spider, *M. aeneolus*.

Based on canopy observations, the most abundant foraging ant species were *C. laevigatus* (72.0%), followed by *Camponotus novaeboracensis* (Fitch) (16.3%), *Formica* spp. (8.3%), and *C. modoc* (3.4%). About 40% of all ants were involved in aphid-tending activities with *Cinara* spp. The proportion of aphid-tending individuals was high in *C. novaeboracensis* (66.3%) and *C. modoc* (76.2%). On the other hand, workers of *C. laevigatus* and *Formica* spp. were more frequently observed actively foraging and fewer individuals were found tending aphids (31.2% and 33.3%, respectively).

A total of 216 prey organisms was collected from ant workers returning to the nests (Table 1). Despite the use of an aspirator in collecting ants, we were only 80–90% successful in removing the prey from the ants. The ants were very cautious and agile, and even a slight disturbance caused them to drop their prey and hide in the nearby vegetation. The most abundant prey organisms brought to the nest were Aphidoidea (48.1%), followed by Psocoptera (12.5%), and Lepidoptera larvae (6.0%) (Table 1). Only three spiders (two lycosids and one salt-

Table 1 Diet composition (number of prey items) of ants and spiders.

Prey group	Ant nests[a]	Ants on foliage	Hunting spiders	Web-building spiders
Diplopoda	2			
Araneae	3	1	1	
Acari	2			
Collembola			2	2
Psocoptera	27	3	2	94
Thysanoptera				1
Hemiptera	4	1		4
Homoptera				
Aphidoidea	104	1		21
Other	5		1	7
Neuroptera[b]	2			
Coleoptera				
Larvae (Coccinellidae)	3	1		1
Adults	2	1		2
Lepidoptera[b]	13			
Diptera				
Larvae	11	2		
Adults	11		2	71
Hymenoptera				
Larvae (Symphyta)	4			
Adults	5			8
Formicidae	9			5[c]
Unidentified	9	1	1	11
Total	216	11	9	227

[a] Pooled data from three nests of *Camponotus laevigatus*

[b] Larvae only

[c] Three *Camponotus* sp. workers captured by an ant specialist *Dipoena nigra* (Emerton); two winged females found in orb webs

icid) were brought to the nests. The most common prey organism in the samples was a bracken fern-feeding aphid, *Sitobion rhamni* (Clarke) (Jensen et al. 1993).

We observed 196 hunting spiders, mostly salticids and philodromids, on foliage in the course of the study. The low number of observations was mostly due to the tendency of these spiders to hide within the Douglas-fir foliage upon a slight disturbance. Only a small proportion of observed hunting spiders was consuming prey (4.6%) (Table 1). We surveyed a total of 215 webs. The majority of the webs was built by sheet-web weavers (53.0%) and orb-weaving spiders (40.5%). The dominant prey groups captured by web spiders were adult Psocoptera (41.4%) and Diptera (31.3%) (Table 1).

The taxonomic composition of prey in spider webs differed significantly from the composition of prey on foliage ($G = 384.6$, $df = 9$, $P < 0.001$), and sticky traps ($G = 326.5$, $df = 9$, $P < 0.001$). Nevertheless, they overlapped substantially (55% and 48%, respectively). Although the taxonomic composition of the diets of web spiders and ants was significantly different ($G = 135.47$, $df = 9$, $P < 0.01$), the overlap in their diets was almost 50%. Both web spiders and ants were capturing prey of similar size distribution (DN = 0.26, $P = 0.41$), with diets overlapping 69%. The limited information on the diet of hunting spiders did not allow us to make meaningful comparisons of their diet with that of ants.

Discussion

Foraging by ants

The increased abundance of arthropod prey in the canopies of ant-free trees suggests that ant foraging had a significant impact on the foliage-dwelling arthropod community. The importance of ant foraging in Douglas-fir canopies was also supported by the composition of the prey sample collected at ant nests. After the bracken fern-feeding aphids, the second most abundant prey organism brought to the nests was a canopy-dwelling psocid, *T. conterminus*.

Only a small percentage of the ants was observed carrying visible prey. Low frequencies of workers carrying visible particles in their mandibles (0.96–6%) have been reported also for *Camponotus pennsylvanicus* (DeGeer) (Sanders 1972; Fowler and Roberts 1980). It has been suggested that, besides honeydew, part of the captured prey is transported to the nest in the ant's crop in the form of hemolymph and water-soluble proteins (Ayre 1963; Fowler and Roberts 1980). Consequently, observations of ants would underestimate the level of foraging based on the presence of visible prey. In addition, the foraging activity of some *Camponotus* species can shift seasonally into the night hours, with some species becoming largely nocturnal (Sanders 1972; Fowler and Roberts 1980). Since our foliage observations were limited to the daytime, we could not evaluate the frequency of nocturnal ant foraging.

Ants may also indirectly limit the abundance of some arthropod groups in the canopy. For example, we observed that ants were extensively palping and licking needles, presumably collecting aphid honeydew accumulated on the foliage. Besides ants, this valuable energy source is also utilized by a variety of other insects [e.g., Johnson and Stafford 1985 (Lepidoptera); Downes and Dahlem 1987 (Diptera); Elliott et al. 1987 (parasitic Hymenoptera)]. In addition, the honeydew may also promote the growth of molds and fungi, as well as function as an adhesive trap for airborne material such as algae, pollen, and organic debris, all of which are widely utilized by foliage-dwelling psocids as a food source (Broadhead and Thornton 1955; New 1970). For example, New (1970) suggests that the amount of honeydew on foliage may be one of the factors affecting the distribution of psocopterans on some British tree species. Consequently, the removal of ants may have increased the availability of this resource to the psocid-dominated arthropod complex in the canopy.

The use of sticky barriers was not expected to limit significantly the dispersal of spiders into the canopy because of their well-developed abilities to balloon (Duffey 1956; Greenstone et al. 1987; Bishop and Riechert 1990) and to disperse on silken bridges among tree canopies (Turnbull 1973). Furthermore, elimination of the cursorial dispersal mode does not appear to have significant effects on the densities (Bishop and Riechert 1990) or community structure (Ehmann 1994) of newly established spider assemblages. We observed that ants were by far the major walking arthropod predators which disperse on tree trunks. Furthermore, if the sticky bands interfered significantly with spider dispersal, we would expect that cursorial hunting spiders would be more likely to be adversely affected by this hurdle than sedentary web builders. This does not appear to be the case; on the contrary, the density of hunting spiders increased in ant-free trees treated with Tanglefoot.

There were no differences in the availability of flying prey organisms between the treatments. The increased abundance of psocids in ant-free canopies was not reflected in significantly higher sticky-trap catches. Though a percentage of the population is winged, their relative scarceness on sticky traps may be due to their limited tendency to fly (Broadhead and Thornton 1955; J. Halaj, personal observation). Thus any observed responses of spiders to the removal of ants could be attributed either to an increase in the psocid-dominated prey complex on the foliage, or to an absence of antagonistic interactions between ants and spiders, or both.

Exploitative competition for prey between spiders and ants

Accumulating observational and direct experimental evidence indicate that some spider populations experience shortages of food, and consequently higher densities of spiders may be found in patches of increased prey densities (see review in Wise 1993). In our study, the abundance of additional prey in ant-free trees should be reflected by one or more of the following: (1) increased densities of spiders; (2) increased feeding rates; (3) larger body sizes; (4) increased reproductive rates. The abundance of hunting spiders in our study appeared to respond to an initial build-up of the prey population on foliage, and subsequently their increased densities appeared to suppress prey populations back to the control level in late September. This could be taken as indirect evidence that food was of limited supply to hunters. However, the limited amount of capture rate information for hunting spiders ($n = 9$), and the absence of direct evidence of food limitation in Douglas-fir-inhabiting spiders do not provide enough evidence to conclude that there is exploitative competition occurring between ants and hunting spiders in this system. In addition, the increased abundance of prey on foliage did not translate into a larger average body size of hunters, which suggests that food may not have been the primary cause of increased densities of hunters in ant-free canopies.

Both ants and web spiders consumed prey of similar size and taxonomic composition. The Psocoptera, Homoptera, and Diptera were well represented in the diets of both groups of predators. Despite the increase in availability of prey on foliage on ant-free trees, the densities and body sizes of web-building spiders remained the same in both treatments, and in fact, there was even a slight tendency for a smaller body size of web-building spiders in ant-free trees ($P = 0.074$).

The response of web-building spiders to elevated densities of prey is not always an easily predictable process (Wise 1993). For example, experimental removals of *Anolis* lizards led to increased densities of available prey and a significantly higher abundance of food-limited web spiders on small islands in the Caribbean (Pacala and Roughgarden 1984; Schoener and Spiller 1987; Spiller and Schoener 1988, 1990). Similarly, aggregation levels of an orb-weaver, *Nephila clavipes* (L.), can be lowered by experimentally reducing its natural supply of prey (Rypstra 1985). On the other hand, however, some spider populations, even though experiencing food shortages, may not exhibit a clear response to higher availability of prey (Wise 1993). For example, Wise (1975, 1979, 1983) has demonstrated food limitation in a sheet-web weaving and in orb-weaving spiders; yet, an artificially increased supply of prey to groups of these spiders did not lower their emigration rates in comparison with groups at natural levels of food supply.

The availability of food for spiders increased in ant-free trees. Nevertheless, the lack of numerical response in web-building spiders combined with the lack of increase in their average body size strongly suggests that the food was not in limiting supply to this spider group. These observations imply that exploitative competition for prey with ants is not likely.

It may have been possible that factors other than food limited the abundance of web spiders in this study. Besides food, web-building spiders are dependent on the quality and availability of the substrate providing web-attachment sites (e.g. Schaefer 1978; Rypstra 1983; Uetz 1991), and an experimental study conducted at a nearby plantation demonstrated the importance of needle density and branching complexity of Douglas-fir foliage to several groups of web-building spiders (Halaj 1996).

Interference competition and predation between spiders and ants

We commonly observed aggressive behavior of ants towards other arthropods on foliage. Twice we observed ants attacking much larger bald-faced hornets, *Dolichovespula maculata* (L.), that collected honeydew on the foliage. The hostility of ants towards other arthropods generally results from their natural predatory behavior and from their mutualistic interactions with homopteran insects (Way 1963). Numerous studies have documented aggressive behavior of homoptera-tending ants towards other predators (e.g. El-Ziady and Kennedy 1956; Bristow 1984; Bach 1991). We observed that about 40% of all ants on the foliage were tending aphids, which may partly account for the aggressive behavior of ants in the canopy.

Both hunting and web-building spiders share the foliage microhabitat with ants, which opens up a possibility of mutual interactions. However, the active foraging of hunting spiders makes them more likely to interact directly with ants. On several occasions, we observed encounters between foraging ants and hunting spiders. For example, visually oriented jumping spiders actively avoided an approaching ant by backing up and rapidly moving away to the opposite side of the twig. If the ant continued in the direction of the escaping spider, the spider dropped on a silken thread and ballooned away from the canopy. A similar "dropping" reaction can also be easily induced by a slight physical contact in groups with less-developed vision such as thomisids, philodromids, or nocturnal hunters, as well as orb-weaving spiders (J. Halaj, personal observation). Dropping as a survival mechanism to escape foliage-foraging ants has also been observed in insects, including the larvae of the jack-pine budworm, *Choristoneura pinus* Freeman (Allen et al. 1970; Jennings 1971) and Douglas-fir tussock moth (Mason and Torgersen 1983). It appears that hunting spiders use an effective escape mechanism to avoid predation by foraging ants. However, escaping spiders usually initiated dispersal, an activity which represents considerable risk for the spider (Wise 1993).

The situation may be different for web-building spiders, which are typically sit-and-wait predators. Brüning (1991) observed that foraging *Formica polyctena* Först. workers are not able to recognize spiders sitting motionless in webs as potential prey. On the other hand, this behavior does not appear to provide protection against predators such as lizards (Schoener and Toft 1983). It appears that the foraging strategy of web-building spiders may provide a selective protection against some predators.

Ants were apparently not able to capture a substantial number of spiders in tree canopies. Similarly, Brüning (1991) concluded that predation by *Formica* on ground-dwelling spiders was "relatively ineffective." Spiders represented only 4.6% of all prey organisms brought to the nest of this ant species. On the other hand, Petal and Breymeyer (1969) estimated that spiders constituted 11–38% of prey captured by meadow-inhabiting *Myrmica* ants. The authors, however, did not provide any direct evidence on the impact of ant foraging on the local spider fauna.

Foraging by ants did not significantly affect spider species richness and diversity. In addition, the significant increase in the absolute abundance of hunting spiders was not strong enough to significantly alter the spider community structure. Similar results have been reported by van der Aart and de Wit (1971). The authors did not find any differences in the total number of spider species between two parts of a meadow, one of which had a great abundance of foraging *Formica rufa* L. On the other hand, Cherix and Bourne (1980) reported higher spider species richness outside a super-colony of *F. lugubris*. It is unclear, however, whether this was a result of ant foraging. Unfortunately, the nonmanipulative nature of both studies and a lack of replication make interpretation of these observations difficult.

In conclusion, this study demonstrated that ant exclusion resulted in a significant increase in the biomass of foliage-dwelling prey organisms. Consequently, the density of hunting spiders increased significantly in these ant-free trees. We did not conclusively demonstrate that spiders profited directly from increased abundance of prey, and were therefore directly competing with ants for food in Douglas-fir canopies. On the other hand, the aggressive behavior of foraging ants appeared to be a source of disturbance to hunting spiders. Disturbed spiders usually initiated dispersal, which may have been a reason for their lower densities in control trees. Direct predation by ants on spiders appeared to be of minor importance in this canopy system. We suggest that this is mostly due to an efficient escape mechanism of hunting spiders (dropping on silken lines), and a unique foraging strategy of web-building spiders (protection provided by webs). This is supported by our observations and a low frequency of spiders in the ant diet.

Polis and McCormick (1986) emphasize the role of direct predation by scorpions in reducing spider densities in a California desert. Similarly, predation by *Anolis* lizards is assumed to be more important than competition for food in reducing the abundance of web-building spiders in the Caribbean (Spiller and Schoener 1988, 1990). The results of our study suggest that interference competition is the primary interaction between ants and hunting spiders in tree canopies. Our findings partly confirm the negative associations between the densities of spiders and ants in young Douglas-fir plantations in western Oregon as suggested by the correlative data. In this study, however, we did not find any evidence of an adverse effect of foraging by ants on web-building spiders. Perhaps the observed negative association between these two groups of predators does not reflect a cause-and-effect interaction, and may have resulted from a differential response to a third environmental variable.

To our knowledge, this study provides the first direct experimental evidence for the existence of competitive interactions between two of the most abundant terrestrial predators. Clarification of the mechanisms of competition between spiders and ants, and its occurrence in other terrestrial communities, requires further testing.

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