The effect of prey availability on spider assemblages on European black pine *[Pinus nigra)* bark: spatial patterns and guild structure

Roland Horvath, Szabolcs Lengyel, Csaba Szinetar, and Laszlo Jakab

Abstract: Both habitat structural complexity and prey availability can influence the density and diversity of spider assemblages. We studied whether prey availability affects spider assemblages living on the bark of European black pine *(Pinus nigra* Arnold) in six localities in Hungary. We found both positive and negative relationships between spider and prey assemblages in a sample of 1290 spiders and 24 186 potential prey when among-locality variation in spider assemblages was controlled for. Species richness, number of individuals, and diversity of spiders increased with either the number of prey taxa or the number of prey individuals in a forest in western Hungary. Spider species richness and number of individuals increased with prey diversity but decreased with number of prey taxa in moderately air-polluted urban localities. There was a negative relationship between number of spider individuals and number of prey individuals in a heavily polluted urban locality. Numbers of nocturnal hunters but not diurnal hunters or web-builders increased with the number of their respective prey in the forest in western Hungary and in the moderately air-polluted urban localities. The number of exclusive bark-dwelling spiders increased with the number of prey individuals in forests in eastern Hungary and decreased with the number of prey individuals in the polluted urban locality. We suggest that patterns of spider assemblages can be influenced by prey availability and that other factors (e.g., habitat structural diversity and air pollution) also need to be considered in explaining these patterns.

Resume : La complexity de la structure de l'habitat et la disponibilite des proies peuvent toutes deux influencer la densite et la diversite des peuplements d'araignees. Nous avons examine comment la disponibilite des proies affecte les peuplements d'araignees vivant sur l'ecorce du pin noir *(Pinus nigra* Arnold) a six sites de Hongrie. II existe des relations positives et negatives entre les peuplements d'araignees et de proies dans un echantillon de 1290 araignees et de 24 186 proies potentielles, une fois que Ton tient compte de la variation des peuplements d'araignees entre les sites. Dans une foret de l'ouest de la Hongrie, la richesse en especes, le nombre d'individus et la diversite des araignees augmentent en fonction ou du nombre de taxons de proies ou du nombre de proies individuelles. Dans les sites urbains a pollution atmospherique moderee, la richesse en especes et le nombre d'individus augmentent chez les araignees en fonction de la diversite des proies, mais diminuent en fonction du nombre de taxons de proies. II existe une relation negative entre le nombre d'individus et le nombre de proies individuelles dans le site urbain fortement pollue. Les araignees chasseresses nocturnes, mais non les chasseresses diurnes, ni les constructrices de toiles, augmentent leur densite en fonction de leurs proies respectives dans la foret de l'ouest de la Hongrie et dans les sites a pollution atmosph6rique moderee. Le nombre d'araignees qui vivent exclusivement sur les ecorces augmente en fonction du nombre de proies individuelles dans les forets de Test de la Hongrie et decroit en fonction du nombre de proies individuelles dans le site urbain pollue. Nous croyons que la structure des peuplements d'araignees peut etre influencee par la disponibilite des proies, mais qu'il faut aussi tenir compte d'autres facteurs explicatifs, tels que la diversite structurale de l'habitat et la pollution atmospherique.

[Traduit par la redaction]

Introduction

Trophic relationships are one of the most important factors determining the composition of communities because populations interact mainly through their feeding relationships (Ricklefs and Miller 1999). For example, prey availability largely affects predator distribution, leading to variation in the number of predators (numerical response), or predators can switch to alternative prey when the availability of their primary prey decreases below a certain threshold

---

Received 7 July 2004. Accepted 13 January 2005. Published on the NRC Research Press Web site at http://cjz.nrc.ca on 29 April 2005.

R. Horvath.[1] Department of Evolutionary Zoology and Human Biology, University of Debrecen, H-4032 Debrecen, Egyetem ter 1, Hungary.
S. Lengyel. MTA-DE Evolutionary Genetics and Conservation Biology Research Group, Department of Evolutionary Zoology and Human Biology, University of Debrecen, H-4032 Debrecen, Egyetem ter 1, Hungary.
C. Szinetar and L. Jakab. Department of Zoology, Berzsenyi College, H-9701 Szombathely, Karolyi G. ter 4, Hungary.

[1] Corresponding author (e-mail: horvathr@tigris.unideb.hu).

Can. J. Zool. 83: 324-335 (2005) doi: 10.1139/Z05-009

(functional response) (Holling 1959; Wise 1993). Understanding the response of predators to prey availability is crucial when unraveling how the interactions between predators and prey influence the composition and structure of communities. These interactions, however, need to be evaluated in light of the ecological setting in which they take place because their strength depends on other factors (e.g. habitat structure, disturbance).

Spiders (Araneae) are ubiquitous and important generalist predators in most terrestrial ecosystems. Spider assemblages are thought to be influenced primarily by habitat structural diversity and secondarily by prey availability and abundance (Halaj et al. 1998, 2000; Nyffeler and Sunderland 2003). Hunting and web-building spiders were found to show the strongest response to changes in habitat structural diversity in a meta-analysis of the effect of structural habitat diversity on invertebrates (Langellotto and Denno 2004). It could not be confirmed that this is effected by higher prey availability in more complex habitats (Langellotto and Denno 2004), i.e., habitat structural diversity per se may be important for spider assemblages. Floristically more diverse Scots pine *(Pinus sylvestris* L.) plantations hosted more spider species than did structurally less complex lodgepole pine *{Pinus contorta* Dougl. ex Loud.) plantations at both the ground level and the canopy level (Docherty and Leather 1997). Because farms are smaller, agricultural habitats are more diverse in northern Europe than in North America, which corresponds to higher densities of small web-building spiders in northern Europe (Nyffeler and Sunderland 2003). The strong relationship between habitat structural diversity and structure of spider assemblages has led some authors to propose that changes in spider community structure can be used for bioindication purposes, mostly to detect human disturbances (Marc et al. 1999).

However, few studies support the view that, in addition to habitat complexity, prey availability can influence the presence/absence and density of spiders within a habitat. For example, in a review of spiders and various pests of coniferous forests, the availability of moths (Tortricidae, Lymantridae, Lasiocampidae) was found to be the main influence on spider assemblages (Bogya and Mols 1996). In western Oregon, the availability of prey (Apioidea, Psocoptera, Diptera, and Collembola) was found to influence the structure of spider communities because higher spider densities were related to higher prey availability on each tree species studied (Halaj et al. 1998). Prey availability, however, explained a smaller, but still significant, proportion of the total variance in spider numbers and diversity than did habitat structure (Halaj et al. 1998). Nevertheless, all arboreal spiders were shown to be limited by strong bottom-up forces in Douglas-fir *(Pseudotsuga menziesii* (Mirbel) Franco) canopies (Halaj et al. 2000).

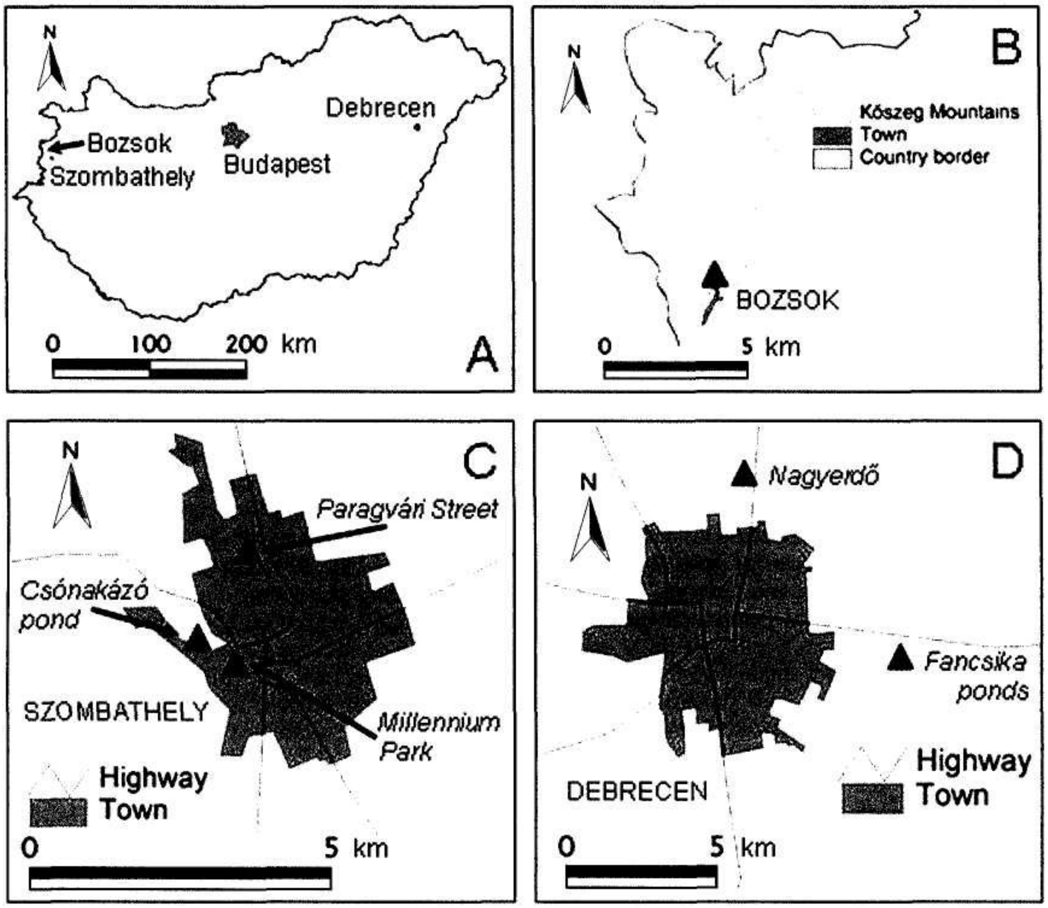
The potential prey of spiders encompasses most invertebrate taxa of similar or smaller sizes that are present in the habitat (Nentwig 1987). However, the spectrum of available prey for spiders differs according to their hunting method and habitat selection. For example, ground-dwelling spiders consume more Collembola and Hymenoptera but fewer Diptera and Hemiptera than do species that hunt on vegetation (Nentwig 1987). Active hunters living on vegetation mostly prey on animals that use the plant surfaces permanently, whereas web-building spiders tend to prey mostly on flying prey ("tourists", sensu Moran and Southwood 1982). The preference of a number of spider species for certain prey taxa or a prey type has been well demonstrated by laboratory studies (Li et al. 1997, 1999; Riechert and Lawrence 1997; Jackson et al. 1998; Jackson 2000). However, the preference shown under controlled conditions may differ from that prevailing in the wild (Herberstein 1996). Thus, several authors have used potential prey (i.e., prey present in the habitat) to characterize spiders' habitat choice (Nentwig 1987; Bardwell and Averill 1997; Crouch and Lubin 2000; Harwood et al. 2001) rather than what they consume under controlled conditions.

Although there is plenty of evidence that habitat structural diversity influences spider assemblages, there are few examples showing a direct link between variation in prey availability and variation in spider assemblages. Either the effect of prey abundance on spiders was of secondary importance to that of habitat structural diversity (Halaj et al. 1998), or spiders and potential prey were linked in structurally poor agroecosystem habitats (Harwood et al. 2001, 2003; Ibarra-Nunez et al. 2001). To our knowledge, there is no published study on the relationship between spiders and their prey from natural habitats where habitat diversity is low.

The aim of this study was to determine the spatial and temporal (seasonal) variation in assemblages of spider species and examine the relationship between the variation in spider assemblages and the variation in prey availability (number of individuals, number of taxa, and prey diversity). We specifically addressed the following questions: *(i)* Are there differences in spider or prey assemblages living on the bark of European black pine *(Pinus nigra* Arnold) among localities in forests (eastern and western Hungary) and a city (western Hungary) and between seasons (summer and fall)? *(ii)* Is there a relationship between the spider assemblages in terms of number of individuals, species richness and diversity, and their prey collected by trunk traps at these localities? *(Hi)* Is there a relationship between species richness and number of spiders belonging to the main guilds (diurnal hunters, nocturnal hunters, and web-builders) and their respective potential prey? *(iv)* Do exclusive or facultative bark-dwelling spiders differ in their numerical response to prey abundance? We used data collected by trunk traps fixed separately for spiders and their prey on the bark of black pine trees to answer these questions.

Trees are highly complex, structurally diverse natural habitats. In general, the bark is structurally less complex than the canopy, therefore habitat complexity can be expected to have only a minor influence on spider assemblages on the bark compared with the canopy. Despite the high number of bark-dwelling spider species, they are rarely studied (e.g., Albert 1976; Wunderlich 1982; Nicolai 1986; Hansen 1992; Szinetar 1992; Simon 1995; Koponen 1996). Most spiders use tree bark only temporarily (e.g., for overwintering; facultative bark-dwelling species), whereas others spend their entire life cycle as bark-dwellers (Wunderlich 1982). Special microclimatic and structural conditions allow the occurrence of various prey taxa on pine tree bark. Many taxa use the bark as their exclusive habitat (e.g., some Pseudoscorpiones, Acari, Dermaptera, Psocoptera, Thysanoptera, Heteroptera, Auchenorrhyncha, Sternorrhcyncha, and Coleoptera). The

Fig. 1. Geographical locations where spiders were sampled from European black pine *(Pinus nigra)* bark in Hungary (A). One forest locality was near Bozsok (B), three urban localities were in Szombathely (C), and two forest localities were near Debrecen (D). Sampling localities are indicated by triangles and their names are italicized.



availability of these insects may largely determine the identity and quantity of spiders using the tree bark.

Material and methods

Study area and sampling

Spiders and their potential prey were collected in 1999 at three urban sites in the city of Szombathely (UTM coordinate XN23) and three forest sites, one in western Hungary, near the village of Bozsok (XN14) and two in eastern Hungary, Nagyerdo forest (ET46) and Fancsika ponds (ET56) (Fig. 1). The six sites, at all of which black pines were planted between 1940 and 1950, are as follows: (1) Millennium Park (formerly Gagarin Avenue), Szombathely: the sampling site is in a park along an avenue surrounded by residential areas. There is little traffic at the edge of the park, and the immission load from air pollution is minimal (see Horvath et al. 2001). Trees are of medium height (ca. 12-15 m), and the foliage, starting ca. 5 m above the ground, is dense and well-developed; (2) Paragvari Street, Szombathely: black pines are located along a main road, and because of heavy traffic, the immission load is high. The trees are relatively short (10-12 m) and their well-developed foliage is located ca. 5 m above the ground; (3) Csonakazo pond, Szombathely: this site is also in a park area and pine trees are located along a minor road between an artificial pond and an open-air swimming pool. There is little traffic and the site is moderately polluted. The trees are short (10-12 m) and their well-developed foliage starts 4-5 m above the ground; (4) Koszeg Mountains, Bozsok: this site is in the southern part of the mountains, ca. 200 m above sea level near the village of Bozsok. The large black pine forest is free from air pollution or other disturbances. The trees are taller (15-20 m) and closer to each other than those in the city sampling sites, and their sparse foliage is located higher (12-14 m) above the ground; (5) Nagyerdo Forest, Debrecen: a large black pine plantation surrounded by deciduous forests, 200 m from a highway with heavy traffic north of the city of Debrecen. Despite the heavy traffic, the immission load is moderate, owing to the filtering effect of the forest. The forest is less dense, trees are of medium height (12-15 m), and the moderately developed foliage starts 7-8 m above the ground; (6) Fancsika ponds, Debrecen: this sampling site is located east of the city of Debrecen and is surrounded by ponds. The immission load is low because the site is far from highways and industrial plants. The forest is also rela-

Table 1. List of spider species collected on the bark of European black pine *(Pinus nigra)* in six sampling localities in Hungary, by family.

	Presence on bark"	Guild group*	No. of individuals
Segestriidae			
Segestria bavarica C.L. Koch, 1843	F	Nocturnal hunter	43
Segestria senoculata (L., 1758)	F	Nocturnal hunter	36
Dysderidae			
Harpactea hombergi (Scopoli, 1763)	F	Nocturnal hunter	36
Harpactea rubicunda (C.L. Koch, 1838)	F	Nocturnal hunter	10
Theridiidae			
Achaearanea riparia (Blackwall, 1834)	F	Web-builder	1
Keijia tincta (Walckenaer, 1802)	F	Web-builder	33
Steatoda bipunctata (L., 1758)	F	Web-builder	57
Theridion blackwalli O. P.-Cambridge, 1871	F	Web-builder	19
Theridion mystaceum L. Koch, 1870	E	Web-builder	7
Theridion pinastri L. Koch, 1872	F	Web-builder	8
Linyphiidae			
Moebelia penicillata (Westring, 1851)	E	Web-builder	181
Tetragnathidae			
Zygiella sp.	A	Web-builder	3
Araneidae			
Larinioides ixobolus (Thorell, 1873)	A	Web-builder	2
Nuctenea umbratica (Clerck, 1757)	E	Web-builder	61
Dictynidae			
Dictyna sp.		Web-builder	3
Amaurobiidae			
Amaurobius fenestralis (Stroem, 1768)	E	Web-builder	39
Amaurobius jugorum L. Koch, 1868	E	Web-builder	1
Anyphaenidae			
Anyphaena accentuata (Walckenaer, 1802)	F	Nocturnal hunter	14
Clubionidae			
Clubiona corticalis (Walckenaer, 1802)	E	Nocturnal hunter	39
Clubiona leucaspis Simon, 1932	E	Nocturnal hunter	57
Clubiona pallidula (Clerck, 1757)	F	Nocturnal hunter	366
Gnaphosidae			
Micaria subopaca Westring, 1861	E	Nocturnal hunter	18
Scotophaeus scutulatus (L. Koch, 1866)	E	Nocturnal hunter	99
Philodromidae			
Philodromus aureolus (Clerck, 1757)	F	Diurnal hunter	15
Philodromus margaritatus (Clerck, 1757)	F	Diurnal hunter	54
Salticidae			
Dendryphantes rudis (Sundevall, 1833)	F	Diurnal hunter	3
Macaroeris nidicolens (Walckenaer, 1802)	F	Diurnal hunter	15
Marpissa muscosa (Clerck, 1757)	E	Diurnal hunter	28
Pseudeuophrys erratica (Walckenaer, 1826)	F	Diurnal hunter	1
Salticus zebraneus (C.L. Koch, 1837)	F	Diurnal hunter	41

"Species were classified as either exclusive bark-dwellers (present on the bark year-round; E) or facultative bark-dwellers (present on the bark from fall to spring; F). 'Guild groups were determined from Szinetar (1992).

tively sparse, the trees are of medium height (12-15 m), and the poorly developed foliage starts 7-8 m above the ground. Spiders were collected by trunk traps made of half-corrugated cardboard strips 15 cm wide wrapped around the tree trunk 3 m above the ground, with the ridged surface facing the trunk, and attached to the bark (Bogya 1995). This method is a standard way of collecting both exclusive and facultative bark-dwelling spider species (Wunderlich 1982). One trunk trap was placed on 10 different trees each site and operated for 10 days at each sampling site. Samples were collected twice: between 2 and 12 July (summer) and between 22 October and 1 November (fall) in the western-Hungary sites, and between 2 and 12 July (summer) and between 6 and 16 November (fall) in the eastern-Hungary sites. Spiders were stored in 70% ethanol and identified to the species level using standard keys (Loksa 1969, 1972; Heimer and Nentwig 1991; Roberts 1995). Species nomenclature follows Platnick (2004). For guild-level analyses, spider

Table 2. Species richness, number of individuals, and Shannon's diversity index (mean ± SD) for spiders collected on the bark of black pine in six localities in summer and fall.

	Species richness	No. of individuals	Shannon's diversity index
Summer			
Millennium Park	3.8 ± 1.75	10.0 ± 4.76	1.11 ± 0.47
Csonakazo pond	4.0 ± 1.15	10.4 ± 3.75	1.17 + 0.31
Paragvari Street	2.7 ± 1.42	4.5 ± 2.01	0.77 ± 0.54
Bozsok	4.0 ± 1.15	11.1 ±4.25	1.24 + 0.31
Nagyerdo forest	1.5 ± 0.85	2.6 ± 2.37	0.35 ± 0.40
Fancsika ponds	2.5 ± 1.26	4.0 ± 1.94	0.75 ± 0.52
Fall			
Millennium Park	5.5 ± 1.49	26.9 ± 24.64	1.24 ± 0.47
Csonakazo pond	6.1 ± 2.33	33.5 ± 42.48	1.26 ± 0.29
Paragvari Street	3.0 ± 3.02	10.8 ± 16.2	0.71 ± 0.63
Bozsok	3.3 ± 2.63	6.9 ± 5.13	0.93 ± 0.69
Nagyerdo forest	1.9 ± 1.10	4.0 ± 3.02	0.50 ± 0.45
Fancsika ponds	2.2 ± 1.69	4.3 ± 4.27	0.63 ± 0.57
Effect^0			
Season ($F_{[U08]}$)	0.38 (0.846)	1.08 (0.302)	0.05 (0.832)
Locality ($F_{[5108]}$)	8.57 (0.001)	12.37 (0.001)	8.56 (0.001)
Interaction ($F_{[5\ 108]}$)	1.94 (0.094)	2.61 (0.029)	0.66 (0.651)

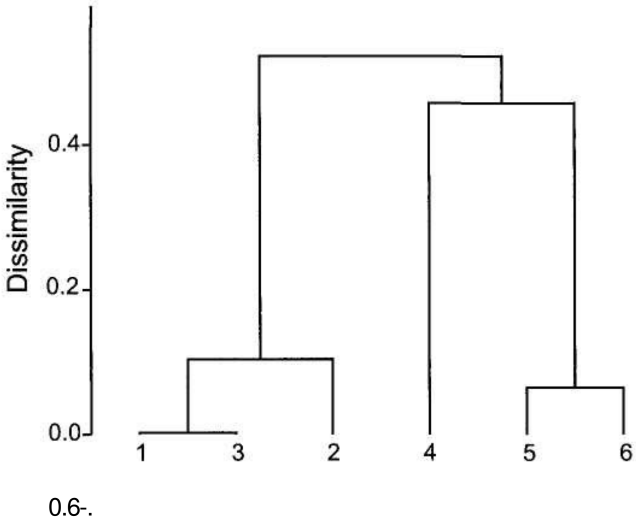
Note: Millennium Park, Cs6nakazo Pond, and Paragvari Street are in the city of Szombathely, Bozsok is a forest in the Koszeg Mountains (western Hungary), and the Nagyerdo forest and Fancsika ponds localities are in lowland forests in eastern Hungary. Twenty traps were used at each locality (*n* = 10 in both summer and fall).

"Two-way ANOVA *F* values (with *p* values in parentheses) are given for the effects (species richness and number of individuals were log transformed).

species were classified into three broad groups: nocturnal hunters, diurnal hunters, and web-builders (Szinetar 1992).

Prey were collected by 5 cm wide trunk traps made of transparent nylon foil (0.2 mm thickness) positioned at a height of 2 m on the same trees where spider traps were installed. The outer surfaces of the traps were made sticky by means of Soveurode aerosol (Sovilo Company, Reims, France). Spider and prey traps were taken off the trees simultaneously in late morning and early afternoon under calm (no wind) conditions. Prey stuck on the nylon foil were identified to the order level using a microscope and standard keys (Ujhelyi 1957, 1959; Steinmann 1970, 1974; Mihalyi 1972; Moczar 1984; Miiller 1985). We followed the nomenclature of Papp (1996). Because spiders in different guilds tend to use different types of prey, prey taxa were divided into *(i)* arthropods living permanently on the bark and *(ii)* "tourists" that visit the bark temporarily (Moran and Southwood 1982). Spiders in the nocturnal-hunter guild chiefly consume permanently bark-dwelling arthropods, whereas the diet of diurnal hunters includes permanent bark-dwellers and tourists that are active during the day and use the bark temporarily (mainly Diptera). Web-builders mostly catch flying tourists but to a lesser extent also catch arthropods dwelling on the bark (Moran and Southwood 1982). Spiders occurring accidentally on the study trees (30 individuals of five species, mostly singletons) were excluded from all analyses.

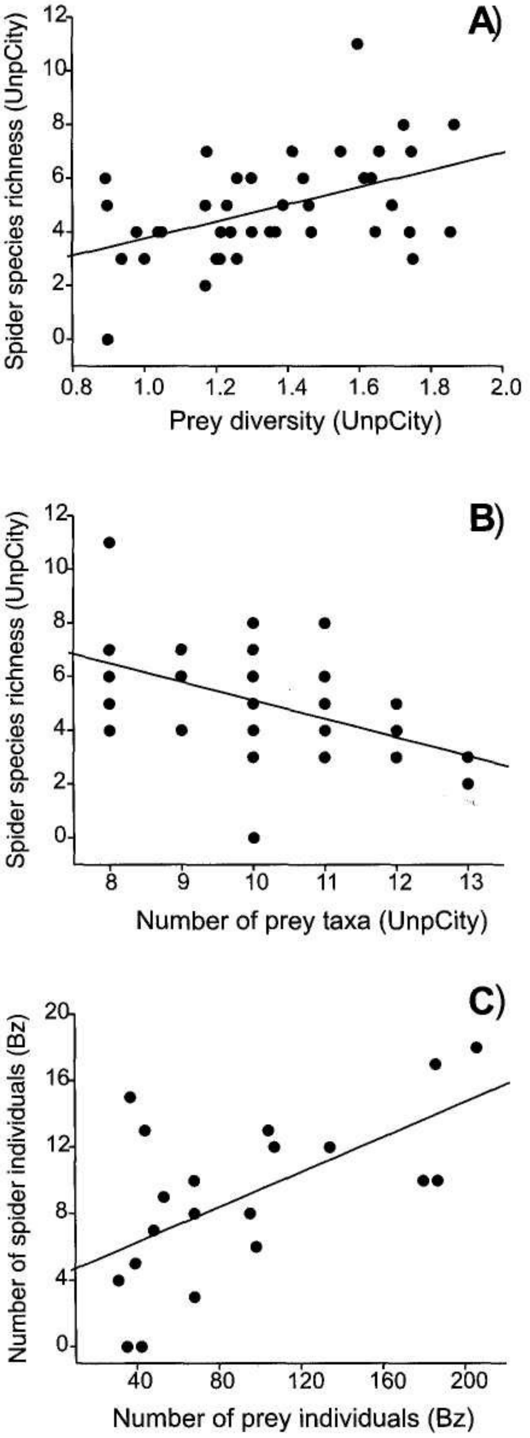
Fig. 2. Dendrogram obtained by a hierarchical cluster analysis of the localities based on the similarity of their spider fauna collected from black pine bark in Hungary. Summer and fall samples were pooled for this analysis. Matusita's index of similarity and the Ward-Orloci fusion method were used. Locations are as follows: 1, Millennium Park; 2, Paragvari Street; 3, Csonakazo pond; 4, Bozsok; 5, Nagyerdo forest; 6, Fancsika ponds.



Statistical analysis

Tree trunk diameter was similar for spider traps and prey traps because traps were positioned ca. 30 cm away from each other on the same tree, and black pine trunks do not change much in diameter within this range of distance. Therefore, we considered the unweighted number of individuals collected in all analyses. Species richness, number of individuals, and spider diversity were tested with two-way full-model ANOVAs with locality and season as fixed fac-

Fig. 3. Relationship between spider species richness and prey diversity (A) (B = 3.19 ± 0.990, R^2 = 0.214, $F_{[138]}$ = 10.374, p = 0.003), between spider species richness and the number of prey taxa (B) (B = -0.69 ± 0.220, R^2 = 0.206, $F_{[1i38]}$ = 9.871, p = 0.003) in the unpolluted urban (UnpCity) localities, and between the number of spider individuals and the number of prey individuals in the Bozsok locality (Bz, forest in western Hungary (C) (B = 0.05 ± 0.017, R^2 = 0.362, $F_{[1>18]}$ = 10.194, p = 0.005) collected from black pine bark.



tors. We used t tests to compare the numbers of spiders in summer and fall samples and corrected for non-equal variances where appropriate by adjusting the degrees of freedom. A hierarchical cluster analysis (Tothmeresz 1993) was used to compare the similarity of spider species assemblages among localities. Linear regression models were fitted to test the relationship between spider species richness, number of individuals, and diversity with the same measures of prey. These models also were used to test the relationships between the number of spider species or individuals and the number of their respective prey within spider guilds (nocturnal hunters, diurnal hunters, and web-builders) and separately for exclusive and facultative bark-dwelling spiders. The diversity of spiders within the guilds was not calculated, owing to the low number of spiders in some localities, which would have led to a biased estimate of spider diversity at the guild level. Parametric tests were used only when the assumptions of such tests were met by the data. Otherwise, data were log transformed to meet these assumptions. For linear regression models, unstandardized coefficients ± SE, F values, and significance are given. Means ± SD and two-tailed probabilities are reported throughout the text.

Results

Spatial and seasonal variation in spider assemblages

We collected a total of 1290 individual spiders belonging to 30 species (Table 1) and 24 186 prey individuals belonging to 5 non-insect orders (Julida, Pseudoscorpiones, Opiliones, Acari, Collembola) and 12 insect orders (Ephemeroptera, Odonata, Dermatoptera, Psocoptera, Thysanoptera, Heteroptera, Auchenorrhyncha, Sternorrhyncha, Coleoptera, Hymenoptera, Lepidoptera, Diptera). The number of spiders per trap was 10.8 ± 17.27 (range 0-150, n = 120 traps), and 11 traps contained no spiders. The number of prey per trap was 201.6 + 130.68 (range 31-615, n = 120).

Spider species richness varied significantly among localities, whereas the effect of season and the interaction term were not significant (Table 2). This was because species richness was lower in Nagyerdo Forest than in other localities (Table 2). There was a significant interaction between locality and season in the number of spiders, but the effect of locality was also highly significant (Table 2). The interaction occurred because the number of individuals increased from summer to fall in the urban localities (summer: 8.3 ± 4.49, fall: 23.7 ± 30.40, t = 2.75, df = 30.3 (corrected for unequal variances), p - 0.010), showed a tendency to decrease in Bozsok (summer: 11.1 ± 4.25, fall: 6.9 ± 5.13, t = 1.99, dfcon-ected - 17.4, p - 0.062), and did not change in localities in eastern Hungary (summer: 3.3 ± 2.23, fall: 4.15 ± 3.60, df = 38, p = 0.375) (Table 2). Shannon's diversity index for spiders also varied significantly among localities, whereas the effect of season and the interaction were not significant (Table 2). The reason for this was that spider diversity was high in two localities in Szombathely and in Bozsok and low in the polluted locality in Szombathely and in eastern Hungary (Table 2).

Species composition in the localities corresponded well to the above results because the unpolluted localities in Szombathely were more similar and were in closer proximity to each other than to the polluted locality, whereas

Table 3. Numbers of individuals (with percentages in parentheses) in the three main spider guilds collected from black pine bark in Hungary.

Locality type	Locality	Nocturnal hunters	Diurnal hunters	Web-builders	Total
Unpolluted city sites	Millennium Park	214 (58.0)	37 (10.0)	118 (32.0)	369
	Csonakazo pond	272 (62.0)	19 (4.3)	148 (33.7)	439
Polluted city site	Paragvari Street	72 (47.1)	8 (5.2)	73 (47.7)	153
Western forest site	Bozsok	132 (73.3)	6 (3.3)	42 (23.4)	180
Eastern forest sites	Nagyerdo forest	23 (34.8)	29 (43.9)	14 (21.3)	66
	Fancsika ponds	47 (56.6)	16 (19.3)	20 (24.1)	83
Total		760 (58.9)	115 (8.9)	415 (32.2)	1290

Bozsok was less similar to the forest sites in eastern Hungary that were similar to each other (Fig. 2).

Based on the spatial and temporal differences and the species set of the localities, we classified the localities into four groups for further analyses. The unpolluted urban localities (Millennium Park and Csonakazo pond) formed the first group (hereinafter UnpCity), the polluted urban locality (Paragvari Street, PCity) and the forest locality in western Hungary (Bozsok) were treated separately, forming the third and fourth groups, and the two forest localities in eastern Hungary (Nagyerdo forest and Fancsika ponds, NF) formed the fourth group.

Relationship between spider and prey assemblages

Spider species richness increased with the number of prey taxa in the Bozsok locality ($B = 0.46 \pm 0.197$, $R^2 = 0.230$, ^[i,i8] - 5.365, $p = 0.033$) and with prey diversity in the UnpCity localities (Fig. 3A). However, spider species richness decreased with the number of prey taxa in the UnpCity localities (Fig. 3B). There were no significant relationships between spider species richness and any other measure of prey abundance at the other localities.

The number of spiders increased with the number of prey taxa in Bozsok ($B = 1.11 \pm 0.502$, $R^2 = 0.214$, $F_{[US]} = 4.905$, p - 0.040). Although the number of spiders decreased with the number of prey taxa in the UnpCity localities (log-transformed number of spiders, B - -0.11 ± 0.041, $R^2 = 0.159$, $F_{[]38]} = 7.201$, $p = 0.011$), the number of spiders increased with prey diversity in these localities (log-transformed number of spiders, $B = 0.47 \pm 0.187$, $R^2 = 0.142$, $F_{[U8]} = 6.314$, $p = 0.016$). The reason for the opposing trends is the negative correlation between the number of prey taxa and prey diversity at these localities (Pearson's correlation, r - -0.377, df = 40, $p = 0.016$). The number of spiders increased with the number of individual prey in Bozsok (Fig. 3C), whereas this relationship was negative in the PCity locality (log-transformed number of spiders, $B = -0.001 \pm 0.001$, $R^2 = 0.199$, $F_{n>18]} = 4.477$, $p = 0.049$). There were no significant relationships between spider number and prey abundance in other localities.

The diversity of spiders increased with both the number of prey taxa and the number of individual prey in Bozsok (log-transformed number of prey taxa: $B = 0.139 \pm 0.051$, $R^2 = 0.291$, $F_{[Um} = 7.391$, $p = 0.014$; number of prey individuals, with log-transformed diversity of spiders, $B = 0.001 \pm 0.000$, $R^2 = 0.205$, $F_{[llS]} = 4.655$, $p = 0.045$). None of the other relationships between spider diversity and prey abundance were significant in the other locations.

Relationship between spider and prey assemblages within spider guilds

Nocturnal hunters were the dominant spider guild in most sampling localities; their proportion was 59% when sites were combined. The proportion of web-builders was lower (32%), while only 9% of spiders collected belonged to the diurnal-hunter guild (Table 3).

The relationships between spiders and the number of their potential prey were statistically significant in the dominant nocturnal-hunter guild. Within this guild, spider species richness increased with the number of prey individuals in the UnpCity localities (Fig. 4A), and both species richness and number of individuals increased with the number of prey individuals in Bozsok (Figs. 4C and 4E, respectively), but not in the other localities. These patterns were similar when all prey without the diurnally active Diptera (see above) and when only bark-dwelling arthropods were considered (UnpCity, species richness: B - 1.073 ± 0.230, $R^2 = 0.233$, $F_{[1>38]} = 11.575$, $p = 0.002$; Bozsok, species richness: $B = 0.898 \pm 2.060$, $R^2 = 0.337$, $F_{\{118]} = 9.154$, $p = 0.007$; number of individuals: $B = 2.097 \pm 1.954$, $R^2 = 0.270$, $F_{[U8]} = 6.643$, $p = 0.019$). No such relationship was found between spiders in the diurnal-hunter and web-builder guilds and their respective prey (total number of prey and bark-dwelling arthropods for diurnal hunters and total number of prey and flying tourists for web-builders) in either of the other localities (Table 4).

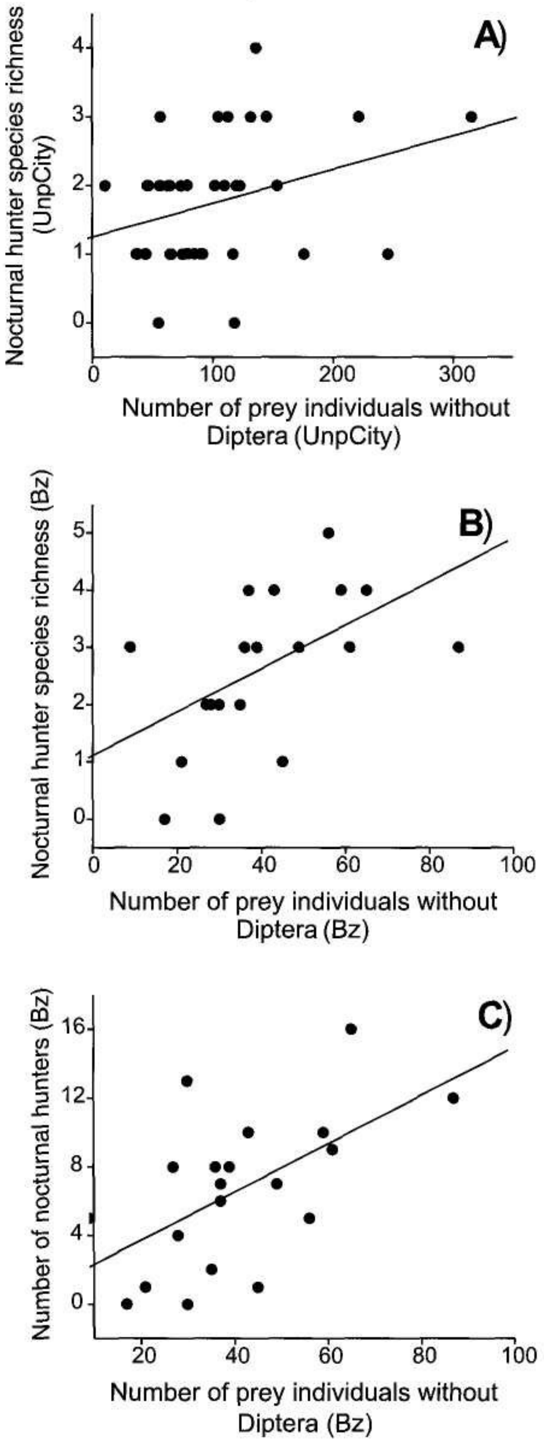
Relationship between exclusive and facultative bark-dwelling spiders and their respective prey

Because exclusive bark-dwellers live on the tree trunk throughout the year, whereas facultative bark-dwellers use the trunk mostly for overwintering, we also tested the relationship between spiders and their prey separately for exclusive and facultative bark-dwellers.

The number of exclusive bark-dwelling spiders decreased with the number of prey individuals in the PCity locality (log-transformed number of spider individuals, $B = -0.002 \pm 0.001$, $R^2 = 0.336$, $F_{[U8,} = 9.092$, $p = 0.007$; Fig. 5A). However, the number of spiders increased with the number of prey individuals in the NF localities combined (log-transformed number of spider individuals, $B = 0.001 \pm 0.000$, $R^2 = 0.180$, $F_{t}i_{>38]} = 8.351$, $p = 0.006$; Fig. 5B).

In contrast, there was no significant relationship between the number of facultative bark-dwelling spiders and the number of prey individuals in either of the localities. Similar results were found when only data from the fall, when facultative bark-dwellers move to the trunk, were analyzed.

Fig. 4. Positive relationships between spider species richness or numbers and numbers of nocturnal hunting spiders and their potential respective prey (excluding Diptera) collected from black pine bark in Hungary, in the unpolluted urban localities (UnpCity) (A) and in the forest in western Hungary (Bozsok, Bz) (B and C). Linear regressions are as follows: A: $B = 1.248 \pm 0.261$, $R^2 = 0.108$, $F_{[1>38]} = 4.622$, $p = 0.038$; B: $B = 1.111 \pm 0.681$, $R^2 = 0.253$, $F_{[U8]} = 6.103$, $p = 0.024$; C: $B = 1.440 \pm 0.637$, $R^2 = 0.201$, $F_{[U8]} = 4.519$, $p = 0.048$.



Discussion

Spider species richness varied significantly among the localities because of the low number of species in one forest locality in eastern Hungary. This area is separated from other black pine plantations by deciduous forests. Smaller spiders that disperse by air may reach the site in smaller proportions than the other localities.

The number of individuals in the urban localities increased from summer to fall, probably because of facultative bark-dwelling spiders coming down the trunk to overwinter (Wunderlich 1982; Horvath et al. 2004). However, the number of spiders in the forest localities decreased or remained stable. Foliage is usually higher and less dense in forests than in urban localities, so spiders can be more dispersed on the tree trunks in forests, resulting in lower spider densities at the height of the trunk traps (3 m) in the forest than in the urban localities. Bird predation may be more intense in forest localities, which may explain why the number of individuals did not increase in the forest localities from summer to fall (cf. Gunnarsson 1988).

The diversity of spiders was low in the eastern-Hungary and PCity locations (Table 2), mostly owing to the fact that species richness and number of individuals were originally low in these localities, probably for the reasons discussed above.

There were significant positive relationships between spider and prey assemblages in the UnpCity and Bozsok localities (Table 4). Spiders may have responded numerically to prey abundance, which may be an important factor in explaining spider abundance in some localities. In Bozsok, for example, each measure of spider abundance was positively related to either the number of prey taxa or the number of prey individuals (Table 4). Prey diversity, however, was positively related to spider species richness and number of individuals only in the UnpCity localities. Thus, there may be several ways in which prey abundance influences spider occurrence and in which spiders may "react" to different measures of prey abundance depending on their way of hunting. In several field studies, conducted in a variety of habitats, evidence of a numerical response between spiders and their prey was also found (Wise 1993). For example, the population of the space web-builder *Achaearanea tepidariorum* (C.L. Koch, 1841) increased with the numbers of potential prey in a Canadian grassland (Turnbull 1964) and spider density was positively related to potential prey density on three out of five tree species in western Oregon (Halaj et al. 1998). The frequency of predation by seven web-building spider species increased with prey availability in coffee plantations (Ibarra-Nunez et al. 2001), and prey availability was significantly higher at actual web microsites of linyphiid spiders than at non-web sites in winter wheat (Harwood et al. 2001). Therefore, under some circumstances, e.g., in structurally less complex habitats, prey availability can play a major role in structuring spider assemblages (Halaj et al. 1998).

In the UnpCity and PCity localities, the occurrence of spiders was negatively associated with prey abundance (number of prey taxa and (or) number of prey individuals; Table 4). These results appear to contradict the previous finding that spiders can be positively affected by prey abundance. How-

Table 4. Summary of the results of linear regression models testing the relationship between species richness, number of individuals, and diversity of spiders and the number of taxa, number of individuals, and diversity of prey collected from black pine bark in four types of locality in Hungary: unpolluted city sites (UnpCity), a polluted city site (PCity), Bozsok (Bz), and eastern forest sites (NF).

Locality type No. of prey taxa No. of prey individuals Prey diversity

	Locality type	No. of prey taxa	No. of prey individuals	Prey diversity
Species richness	UnpCity	(-) (0.003)	0.460	(+) (0.003)
	PCity	0.207	0.094	0.702
	Bz	(+) (0.033)	0.208	0.568
	NF	0.836	0.733	0.572
No. of individuals	UnpCity	H (0.011)	0.581	(+) (0.016)
	PCity	0.574	(-) (0.049)	0.505
	Bz	(+) (0.040)	(+) (0.005)	0.486
	NF	0.518	0.770	0.446
Spider diversity	UnpCity	0.605	0.560	0.207
	PCity	0.630	0.731	0.836
	Bz	(+) (0.014)	(+) (0.045)	0.440
	NF	0.751	0.499	0.386

Note: Statistically significant positive relationships are indicated by (+) and negative relationships by (-); *p* values are given (in parentheses for significant relationships).

ever, there was a negative correlation between the number of prey taxa and prey diversity at the UnpCity localities. The high number of prey taxa on some trees at these localities was caused mostly by high numbers of prey that are presumably consumed by spiders in lower proportions (mostly Diptera), and the dominance of such prey led to a lower prey diversity, which may have resulted in a low spider species richness. On other trees, however, prey were more evenly distributed by taxon, resulting in greater prey diversity and higher numbers of individual spiders and spider species. Thus, under some circumstances, the composition of prey assemblages may explain the abundance of spiders (e.g., Riechert and Lawrence 1997; Denno et al. 2003).

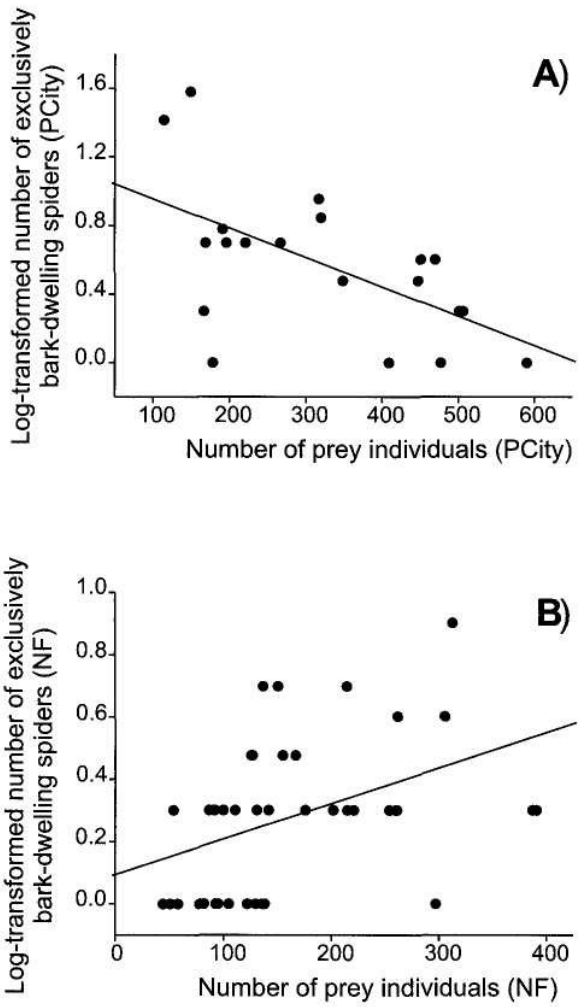
There was a negative relationship between the number of spiders and the number of prey individuals at the PCity location. Air pollution had damaged the bark of many trees and so exposed them to herbivorous insects and pests. This locality also is suboptimal for spiders because of air pollution (Horvath et al. 2001), which may have reduced their abundance, especially on trees more exposed to air pollution. These two effects may explain the negative correlation between the number of exclusive bark-dwelling spiders and prey abundance (Fig. 5A), which also biased the relationship between prey abundance and the entire spider assemblage at this locality. It is unlikely that the negative correlation was caused by the severe depression of prey numbers by spiders because this locality had the highest prey abundance.

In the guild-level analyses, we found positive relationships between spiders and the abundance of their respective prey only for nocturnal hunters. Such relationships were found in the UnpCity and Bozsok localities (Figs. 4A-4C), and both when all prey without Diptera and when bark-dwelling prey were used. In Bozsok, each of the four comparisons (number of individual spiders and spider species with two sets of prey) yielded significant results, whereas in the UnpCity localities only spider species richness was related positively to both sets of prey. We did not find such relationships in the other two spider guilds. One reason for this may be that diurnal hunters were active and would be less likely to stay under the trunk traps at the time the traps were collected (noon), and that the females of web-building species are more or less sessile, and were therefore less likely to move during the sampling period. Our sample (Table 3) contained mostly juvenile web-builders, which hunt on the bark during the day, similar to active hunters, which perhaps explains why there was no relationship between web-building spiders and their potential prey.

Although using alternative guild-classification schemes could further elucidate relationships, the ecological characteristics of the bark-dwelling spiders collected in this study were not various enough to allow a different guild classification to be used. Our classification scheme corresponded well to that proposed by Uetz et al. (1999) based on ecological characteristics. Their stalker/ambusher group corresponds to our diurnal-hunter category (Philodromidae, Salticidae), and the species belonging to their running spider group and collected in this study were all nocturnal (Dysderidae, Anyphaenidae, Clubionidae, Gnaphosidae). The rest of the families collected in this study (Theridiidae, Linyphiidae, Tetragnathidae, Araneidae, Dictynidae, Amaurobiidae) were all web-builders by both classifications. One web-building, nocturnally active family (Segestriidae) was considered a nocturnal hunter in this study because although species of this family build a web, it only serves to signal the passing of prey, which they catch by running.

There was a positive relationship between exclusive bark-dwelling spiders and the number of prey individuals only in the NF localities combined (Fig. 5B). One reason that such a relationship was found only at localities with the smallest number of species but not at the other localities may be that two *(Marpissa muscosa* (Clerck, 1757), *Nuctenea umbratica* (Clerck, 1757)) out of the four exclusive bark-dwelling species at these localities were dominant (representing 45 of the 52 individuals collected), and their numerical response to prey determined the overall relationship at these localities. The effect of individual species on the overall relationship

Fig. 5. Relationship between the number of exclusive bark-dwelling spiders and the number of prey individuals in the polluted urban locality (PCity) (A) and in the forest localities in eastern Hungary (NF) (B).



was probably less important at the other locations, where there were more species.

Despite significant relationships found between spider and prey assemblages, the direction of cause and effect, i.e., whether spiders suppress prey populations or prey influence spider populations remains unclear. Several studies show that spiders exert negative effects on prey populations. For example, the experimental addition of predatory wolf spiders to an assemblage of sap-feeders led to a reduction of sap-feeders belonging to the genus *Prokelisia* Osborn, 1905 (Denno et al. 2003). Some species (e.g. common plant hoppers) were more affected by wolf spiders than other taxa, which demonstrates that various components of a prey community may be affected in different ways through differential predation by spiders (Denno et al. 2003). The results of our observational study do not allow us to establish cause-and-effect relationships, which would require experimental manipulation of either spiders or prey and knowledge of the prey actually consumed.

Spiders are capable of recognising sites with higher prey availability. For example, the sit-and-wait predator *Misumenops argenteus* (Mello-Leitao, 1929) generally occupies sites with high prey frequency (Romero and Vascencellos-Neto 2004), whereas linyphiid spiders place their sheet webs at sites with higher prey availability even in relatively uniform agro-environments (Harwood et al. 2003). Laboratory studies demonstrate that spiders use visual and (or) vibratory cues to assess prey density and spend more time in patches of higher prey density (Persons and Uetz 1998). However, aggregations of spiders and prey can also form in the field simply if they have similar microhabitat preferences, e.g., between two species of dwarf spider and their springtail prey in coastal sand dunes (Bonte and Mertens 2003). Although such a scenario is plausible for a small number of predators and prey, it is rather unlikely in our study, because the wide distribution and high number of prey taxa and spiders of different guilds on black pine bark make the coexistence of common microhabitat preference highly unlikely.

In summary, this study provided evidence of numerical responses between spiders and their potential prey when differences in spider abundance among sampling localities were accounted for. Positive relationships were found between spider and prey abundances for all bark-dwelling spiders (Bozsok forest and UnpCity localities), for nocturnal hunters, the dominant guild (Bozsok and UnpCity localities), and for exclusive bark-dwellers (NF forests). Negative relationships, detected for all spiders (UnpCity and PCity) and for exclusive bark-dwellers (PCity), could be largely attributed either to opposing trends between two measures of prey abundance or to air pollution. Other factors that may affect the composition and distribution of spider assemblages include habitat structural diversity (Halaj et al. 1998), habitat productivity (Shochat et al. 2004), intraguild competition (Shochat et al. 2004), air pollution (Horvath et al. 2001), and predator abundance (Gunnarsson 1988). Our study suggests that trophic interactions between spiders and their potential prey can be important in the organization and quantitative composition of insect communities under certain circumstances, e.g., in a relatively constant, structurally less complex habitat, tree bark.

Acknowledgements

We thank Prof. Zoltan Varga for stimulating discussions during the research and to Szabolcs Honti and Peter Kozma for help in the field. Szabolcs Lengyel was supported by a National Base Programs for Scientific Research (OTKA) grant (F30403) and a Bekesy Postdoctoral Fellowship, and Csaba Szinetar was a Bolyai Fellow of the Hungarian Academy of Sciences during the preparation of the manuscript.

References

Albert, R. 1976. Zusammensetzung und Vertikalverteilung der Spinnenfauna in Buchenwaldern des Soiling. Faun. Oekol. Mitt. 5: 65-80.

Bardwell, C.J., and Averill, A.L. 1997. Spiders and their prey in Massachusetts cranberry bogs. J. Arachnol. 25: 31-41.

Bogya, S. 1995. Clubionid spiders (Clubionidae) as perspective factors in the biological control of apple orchards. Novenyvedelem, **31:** 149-153. [In Hungarian with English summary.]

Bogya, S., and Mols, P.J.M. 1996. The role of spiders as predators of insects pest with particular reference to orchard: a review. Acta Phytopath. Entomol. Hung. **31:** 83-159.

Bonte, D., and Mertens, J. 2003. The temporal and spatial relationship between stenotopic dwarf spiders (Erigoninae, Araneae) and their prey (Isotomidae, Collembola) in coastal grey dunes: a numerical aggregative response or common microhabitat preference? Neth. J. Zool. 52: 243-253.

Crouch, T.E., and Lubin, Y. 2000. Effects of climate and prey availability on foraging in a social spider, *Stegodyphus mimosarum* (Araneae, Eresidae). J. Arachnol. 28: 158-168.

Denno, R.F., Gratton, C, Dobel, H., and Finke, D.L. 2003. Predation risk affects relative strength of top-down and bottom-up impacts on insect herbivores. Ecology, 84: 1032-1044.

Docherty, M., and Leather, S.R. 1997. Structure and abundance of arachnid communities in Scots and lodgepole pine plantations. For. Ecol. Manag. 95: 197-207.

Gunnarsson, B. 1988. Spruce-living spiders and forest decline; the importance of needle-loss. Biol. Conserv. 43: 309-319.

Halaj, J., Ross, D.W., and Moldenke, A.R. 1998. Habitat structure and prey availability as predictors of the abundance and community organization of spiders in western Oregon forest canopies. J. Arachnol. 26: 203-220.

Halaj, J., Ross, D.W., and Moldenke, A.R. 2000. Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. Oikos, 90: 139-152.

Hansen, H. 1992. Uber die Arachniden-Fauna von urbanen Lebensraumen in Venedig — II. Die Rinde-Bewohnenden Arten des Stammbereiches von *Platanus hybrida.* Boll. Mus. Civ. Stor. Nat. Venezia, 41: 91-108.

Harwood, J.D., Sunderland, K.D., and Symondson, W.O.C. 2001. Living where the food is: web location by linyphiid spiders in relation to prey availability in winter wheat. J. Appl. Ecol. 38: 88-99.

Harwood, J.D., Sunderland, K.D., and Symondson, W.O.C. 2003. Web-location by linyphiid spiders: prey-specific aggregation and foraging strategies. J. Anim. Ecol. 72: 745-756.

Heimer, S., and Nentwig, W. 1991. Spinnen Mitteleuropas. Paul Parey Verlag, Berlin and Hamburg.

Herberstein, M.E. 1996. The prey captured by web building spiders (Araneae, Linyphiidae) in comparison with feeding experiments. Rev. Suisse Zool. Vol. Hors Ser.: 279-288.

Holling, C.S. 1959. The components of predation as revealed by a study of small mammal predation on the European sawfly. Can. Entomol. **91:** 293-320.

Horvafh, R., Magura, T., and Szinetar, Cs. 2001. Effects of immission load on spiders living on black pine. Biodivers. Conserv. 10: 1531-1542.

Horvath, R., Lengyel, Sz., Szinetar, Cs., and Honti, Sz. 2004. The effect of exposition time and temperature on spiders (Araneae) overwintering on the bark of black pine *(Pinus nigra). In* European Arachnology 2002: Proceedings of the 20th Colloquium of Arachnology, Szombathely, Hungary, 22-26 July 2002. *Edited by* F. Samu and Cs. Szinetar. Plant Protection Institute and Berzsenyi College, Budapest, pp. 95-102.

Ibarra-Nunez, G., Garcia, J.A., Lopez, J.A., and Lachaud, J.P. 2001. Prey analysis in the diet of some ponerine ants (Hymenoptera, Formicidae) and web-building spiders (Araneae) in coffee plantations in Chiapas, Mexico. Sociobiology, 37: 723-755.

Jackson, R.R. 2000. Prey preferences and visual discrimination ability of *Brettus, Cocalus* and *Cyrba,* araneophagic jumping spiders (Araneae, Salticidae) from Australia, Kenya and Sri Lanka. N.Z. J. Zool. 27: 29-39.

Jackson, R.R., Li, D.Q., Barrion, A.T., and Edwards, G.B. 1998. Prey-capture techniques and prey preferences of nine species of ant-eating jumping spiders (Araneae, Salticidae) from the Philippines. N.Z. J. Zool. 25: 249-272.

Koponen, S. 1996. Spiders (Araneae) on trunks and large branches of oak *(Quercus robur)* in SW Finland. Rev. Suisse Zool. Vol. Hors Ser.: 335-340.

Langellotto, G.A., and Denno, R.F. 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. Oecologia (Berl.), **139:** 1-10.

Li, D.Q., Jackson, R.R., and Barrion, A. 1997. Prey preferences of *Portia labiata, P. africana,* and *P. schultzi,* araneophagic jumping spiders (Araneae, Salticidae) from the Philippines, Sri Lanka, Kenya, and Uganda. N.Z. J. Zool. 24: 333-349.

Li, D.Q., Jackson, R.R., and Harland, D.P. 1999. Prey-capture techniques and prey preferences of *Aelurillus aeruginosus, A. cognatus,* and *A. kochi,* ant-eating jumping spiders (Araneae, Salticidae) from Israel. Isr. J. Zool. 45: 341-359.

Loksa, I. 1969. Pokok I. Araneae I. Akademia Nyomda, Budapest.

Loksa, I. 1972. Pokok II. Araneae II. Akademia Nyomda, Budapest.

Marc, P., Canard, A., and Ysnel, F. 1999. Spiders (Araneae) useful for pest limitation and bioindication. Agric. Ecosyst. Environ. 74: 229-273.

Mihalyi, F. 1972. Ketszarnyuak — Diptera. Akademiai Nyomda, Budapest.

Moczar, L. *{Editor).* 1984. Identification of animals. Vols. I—**II.** [Allathatarozo I—**II.]** Tankonyvkiado, Budapest. [In Hungarian.]

Moran, V.C., and Southwood, T.R.E. 1982. The guild composition of arthropod communities in trees. J. Anim. Ecol. 51: 289-306.

Mtiller, H.J. 1985. Bestimmung wirbelloser Tiere im Gelande. VEB Gustav Fischer Verlag, Jena.

Nentwig, W. 1987. The prey of spiders. *In* Ecophysiology of spiders. *Edited by* W. Nentwig. Springer-Verlag, Berlin, pp. 249-263.

Nicolai, V. 1986. The bark of trees: thermal properties, microclimate and fauna. Oecologia (Berl.), 69: 148-160.

Nyffeler, M., and Sunderland, K.D. 2003. Composition, abundance and pest control potential of spider communities in agroecosystems: a comparison of European and US studies. Agric. Ecosyst. Environ. 95: 579-612.

Papp, L. *{Editor).* 1996. Zootaxonomy. [Zootaxonomia.] Dabas-Jegyzet Kft., Dabas. [In Hungarian.]

Persons, M.H., and Uetz, G.W. 1998. Presampling sensory information and prey density assessment by wolf spiders (Araneae, Lycosidae). Behav. Ecol. 9: 360-366.

Platnick, N.I. 2004. The world spider catalog. Version 4.5 [online]. Available from http://research.amnh.org/entomology/spiders/catalog/index.html [cited 1 July 2004].

Ricklefs, R.E., and Miller, G.L. 1999. Ecology. W.H. Freeman and Co., New York.

Riechert, S.E., and Lawrence, K. 1997. Test for predation effects of single versus multiple species of generalist predators: spiders and their insect prey. Entomol. Exp. Appl. 84: 147-155.

Roberts, M.J. 1995. Spiders of Britain and northern Europe. HarperCollins Publishers, London.

Romero, G.Q., and Vascencellos-Neto, J. 2004. Foraging by the flower-dwelling spider, *Misumenops argenteus* (Thomisidae), at high prey density sites. J. Nat. Hist. 38: 1287-1296.

Shochat, E., Stefanov, W.L., Whitehouse, M.E.A., and Faeth, S.H. 2004. Urbanization and spider diversity: influences of human modification of habitat structure and productivity. Ecol. Appl. 14: 268-280.

Simon, U. 1995. Untersuchung der StratozOnosen von Spinnen und Weberknechten (Arachnoidea: Araneae, Opilionida) an der Waldkiefer *(Pinus sylvestris).* Wissenschaft und Technik Verlag, Berlin.

Steinmann, H. 1970. Rovarok. Insecta. Akademiai Nyomda, Budapest.

Steinmann, H. 1974. Borszarnyuak. Dermatoptera. Akademiai Nyomda, Budapest.

Szinetar, C. 1992. Spruce as spider-habitat in urban ecosystem I. Folia Entomol. Hung. 53: 179-188.

Tothmeresz, B. 1993. NuCoSA 1.0: number cruncher for community studies and other ecological applications. Abstr. Bot. 17: 283-287.

Turnbull, A.L. 1964. The search for prey by a web-building spider *Achaearanea tepidariorum* (C.L. Koch) (Araneae, Theridiidae). Can. Entomol. 96: 568-579.

Uetz, G.W., Halaj, J., and Cody, A.B. 1999. Guild structure of spiders in major crops. J. Arachnol. 27: 270-280.

Ujhelyi, S. 1957. Szitakotok. Odonata. Akademiai Nyomda, Budapest.

Ujhelyi, S. 1959. Kereszek. Ephemeroptera. Akademiai Nyomda, Budapest.

Wise, D.H. 1993. Spiders in ecological webs. Cambridge University Press, Cambridge.

Wunderlich, J. 1982. Mitteleuropaische Spinnen (Araneae) der Baumrinde. Z. Angew. Entomol. 94: 9-21.